

The *Beagle* collections of Darwin's finches (Geospizinae)



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Synopsis

In spite of the importance of the Geospizinae, or 'Darwin's finches', in evolutionary theory, the original type specimens from the *Beagle* voyage have long been a source of puzzlement to ornithologists. More especially, the localities recorded on the specimens do not seem to coincide, in a number of cases, with the various species and subspecies distributions observed today. The explanation for these anomalous specimens lies, in part, in Darwin's own collecting procedures while in the Galapagos. Darwin was initially misled by the divergent nature of these finch species, actually thinking them to be members of several different subfamilies. In addition (and contrary to the legend), Darwin did not begin to separate his ornithological collections by island while he was in the Galapagos Archipelago. Rather, whatever information he later provided in this connection was largely derived, after the *Beagle* voyage, from the carefully labelled collections of three other *Beagle* shipmates. It was at this time that Darwin, impressed by John Gould's (1837*a*) expert ornithological analysis of his Galapagos birds, finally became a convinced evolutionist and realized the closely related nature of the Geospizinae. Darwin's specimens, which were largely unlabelled by island, later acquired a number of erroneous localities as a result of Darwin's own incorrect guesses, as well as the efforts of later ornithologists to make Darwin's specimens agree with his published localities. As for the three other *Beagle* collections of Darwin's finches, these are accurately identified and described here for the first time. Moreover, these collections are shown to clarify a number of important problems bearing on the nomenclature and geographic distribution of Darwin's finches. In particular, hitherto unknown manuscript evidence establishes that a peculiarly large-billed form of *Geospiza magnirostris*, the Large Ground Finch, was collected on Chatham and Charles islands, where the form is now extinct. Another extinct form, *G. nebulosa*, the Sharp-beaked Ground Finch, was collected on Charles Island. *G. magnirostris magnirostris* and *G. magnirostris strenua* are therefore recognized here as valid trinomial, and the name *G. nebulosa* (Gould, 1837*a*) is recognized as having priority over *G. difficilis* (Sharpe, 1888). Finally, a summary table of specifications and measurements regarding the *Beagle* type specimens of Darwin's finches is provided in an appendix.

Introduction

The Geospizinae, or 'Darwin's finches', have inspired an impressive body of scientific research ever since Charles Darwin first collected these birds during the voyage of H.M.S. *Beagle* (1831–36). As a miniature paradigm of evolution in action, the Geospizinae have few ornithological rivals, and they are rightly celebrated today as a classic case of adaptive evolutionary radiation.

Largely responsible for this special scientific status of Darwin's finches is the famous laboratory of evolution—the Galapagos Archipelago—where Darwin encountered these endemic birds in September of 1835. This oceanic archipelago comprises sixteen principal islands located on the equator some six hundred miles west of Ecuador (Fig. 1). Wholly volcanic in origin, the Galapagos Islands are several million years old and have never been connected to the South American mainland. Darwin's finches were evidently one of the earliest colonists of this archipelago, since their degree of evolutionary complexity (thirteen species belonging to four different genera) is unique among Galapagos birds. A fourteenth species belonging to yet another genus inhabits Cocos Island, four hundred miles to the northeast. Because Darwin's finches have no close ancestor on the American mainland, they are classified in their own separate tribe or subfamily, which is placed with the Emberizidae¹.

Being one of the earliest colonists of the Galapagos, the ancestral form of these birds must have encountered a sparsely tenanted environment possessing numerous vacant ecological niches. Through geographic isolation on the different islands, various finch populations gradually evolved reproductive isolation and hence status as separate species. Whenever these similar species were successful in recolonizing neighbouring islands, there ensued competition for scarce resources and eventually divergence and adaptive radiation into more specialized niches. Through this four-part process of geographic isolation, speciation, recolonization, and adaptive radiation, Darwin's finches have evolved a remarkable difference in the form of their beaks. Between the largest bill, which is shaped like that of a grosbeak, and the smallest, which resembles that of a warbler, graduated differences in beak structure are found with every species. There are three species of ground finches with large, medium, and small beaks; a fourth species of ground finch with a sharp, pointed beak; two species of cactus-eating finches; a vegetarian tree finch; large, medium, and small insectivorous tree finches; a mangrove finch; a finch that closely resembles a warbler in both its morphology and behaviour; and finally a tool-using 'woodpecker' finch, which extracts its prey from crevices in tree trunks by using twigs and cactus spines (Fig. 2). It was this striking degree of morphological differentiation that led Darwin to comment in his *Journal of Researches*: 'Seeing this gradation and diversity in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends' (1845 : 380).

Although research on Darwin's finches has continued to contribute in important ways to the understanding of evolutionary theory, there is one problem that has remained largely unresolved ever since Darwin collected these birds in 1835. This problem concerns the type localities of Darwin's own specimens, an issue that has been the subject of repeated discussion and debate in the ornithological literature. Not only have various doubts been expressed about the reliability of Darwin's collecting and recording procedures, but questions of proper nomenclature and even evolutionary issues have also been raised in this context. In addition, this problem is closely associated with a much-discussed historical question, namely, when was it that Darwin first realized the importance of geographic isolation as a key to species formation. Given the fame of this episode in Darwin's life, there has been a surprising degree of misunderstanding and misinformation regarding these issues. In fact, over the years Darwin's finches have become the focus of a considerable legend in the history of science, one that I have examined more extensively elsewhere (1982a). Here I shall confine myself to the problem of clarifying the type localities of the *Beagle* Geospizinae.

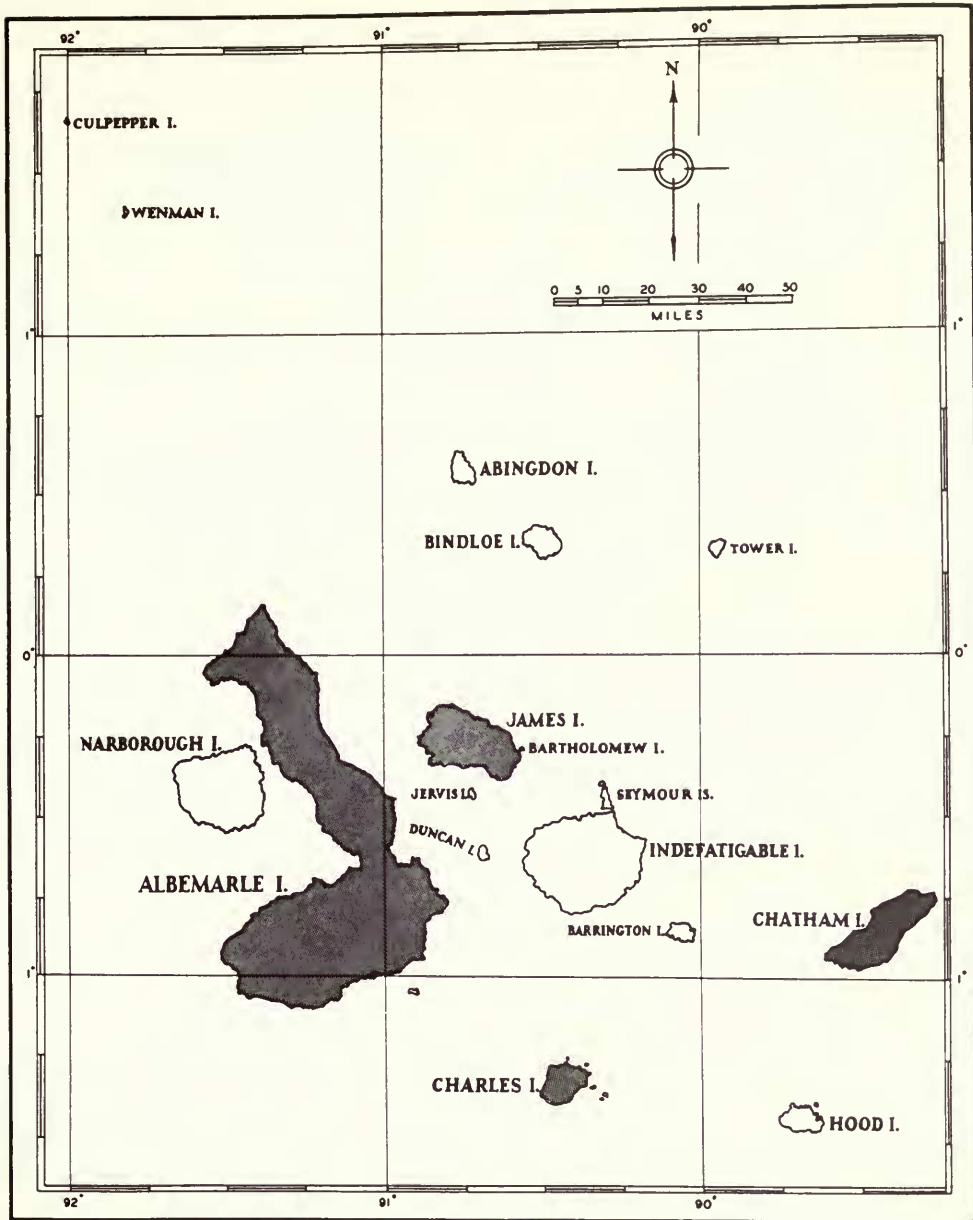


Fig. 1 The Galapagos Archipelago. Darwin visited the four shaded islands. (From Lack, 1945: Frontispiece.)

Darwin in the Galapagos

In his *Journal of Researches* Darwin later reported that the possibility of the different islands possessing separate forms was first brought to his attention by Nicholas O. Lawson, the vice-governor of the archipelago. Lawson, whom Darwin met on Charles Island, informed him that 'the tortoises differed from the different islands, and that he could with certainty tell from which island any one was brought' (Darwin 1845 : 394). This discussion took place sometime between 25 and 27 September 1835, during the second of Darwin's five weeks in the archipelago². 'I did not for some time', Darwin commented, 'pay sufficient attention to

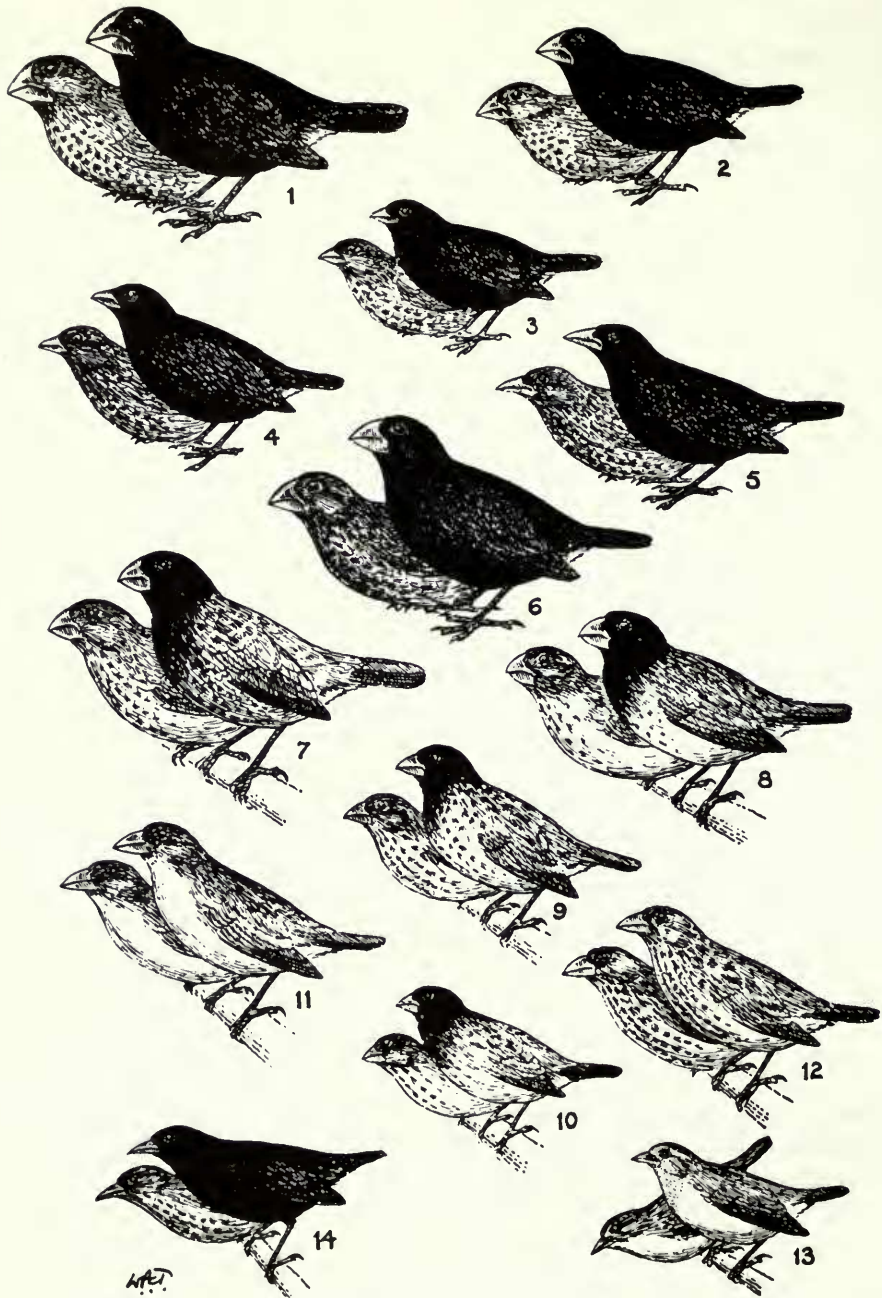


Fig. 2 Darwin's finches; the male (in dark plumage) and female of each species: 1, 2, 3, the Large, Medium, and Small Ground Finches (*Geospiza magnirostris*, *G. fortis*, and *G. fuliginosa*); 4, the Sharp-beaked Ground Finch (*G. nebulosa* [formerly *difficilis*]); 5 and 6, the Cactus and Large Cactus Finches (*G. scandens* and *G. conirostris*); 7, the Vegetarian Tree Finch (*Platyspiza crassirostris*); 8, 9, and 10, the Large, Medium, and Small Insectivorous Tree Finches (*Camarhynchus psittacula*, *C. pauper*, and *C. parvulus*); 11, the Woodpecker Finch (*C. pallidus*); 12, the Mangrove Finch (*C. heliobates*); 13, the Warbler Finch (*Certhidea olivacea*); and 14, the Cocos Island Finch (*Pinaroloxias inornata*). (From Lack, 1947 : 19.)

this statement, and I had already partially mingled together the collections from two of the islands. I never dreamed that islands, about fifty or sixty miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to a nearly equal height, would have been differently tenanted . . . [B]ut I ought, perhaps, to be thankful that I obtained sufficient material to establish this most remarkable fact in the distribution of organic beings' (1845 : 394).

Darwin did fortunately notice that the mockingbird he had collected on Charles Island differed from the form he had previously collected on Chatham Island. This discovery made him pay particular attention to their collection; and he subsequently made efforts to obtain, and to keep separate, specimens from the next two islands he visited (1841 : 63). These next two islands were Albemarle, where Darwin spent only part of a day, and James, where he spent a week. To Darwin's eyes, the mockingbird specimens from Chatham and Albemarle appeared to be the same, but those from James and especially Charles were noticeably different³. In his zoology notes Darwin commented about these specimens at the time: 'This bird which is so closely allied to the Thenca of Chili (Callandra of B. Ayres) is singular from existing as varieties or distinct species in the different Is^{ds}.—I have four specimens from as many Is^{ds}.—There will be found to be 2 or 3 varieties.—Each variety is constant in its own Island.—This is a parallel fact to the one mentioned about the Tortoises.'⁴ It was this singular fact in the distribution of the mockingbirds that subsequently prompted Darwin to write in his *Ornithological Notes*:

When I recollect, the fact that from the form of the body, shape of scales & general size, the Spaniards can at once pronounce, from which Island any Tortoise may have been brought. When I see these islands in sight of each other, & possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. The only fact of a similar kind of which I am aware, is the constant asserted difference—between the wolf-like Fox of East and West Falkland Islds.—If there is the slightest foundation for these remarks the zoology of Archipelagoes—will be well worth examining; for such facts [would inserted] undermine the stability of Species. (1963[1836] : 262)

This famous statement, written approximately nine months after leaving the Galapagos Archipelago, is Darwin's first tentative admission of the possibility that species might be mutable⁵.

To what extent, then, did the finches help to reinforce this insight? According to David Lack (1947 : 23), Darwin also began to separate the members of the finch tribe as a result of the vice-governor's remarks to him on Charles Island. Thereafter, Lack maintains, Darwin kept his ornithological collections from each island separate. Lack's assertion is based on a detailed examination of Darwin's type specimens, many of which are labelled as coming from the last island Darwin visited, and on the following statement made by Darwin in his *Journal of Researches*:

Unfortunately most of the specimens of the finch tribe were mingled together; but I have strong reasons to suspect that some of the specimens of the sub-group Geospiza are confined to separate islands. If the different islands have their representatives of Geospiza, it may help to explain the singularly large number of the species of this sub-group in this one small archipelago, and as a probable consequence of their numbers, the perfectly graduated series in the size of their beaks. Two species of the sub-group Cactornis, and two of Camarhynchus, were procured in the archipelago; and of the numerous specimens of these two sub-groups shot by four collectors at James Island, all were found to belong to one species of each; whereas the numerous specimens shot either on Chatham or Charles Island (for the two sets were mingled together) all belonged to the two other species: hence we may feel almost sure that these islands possess their representative species of these two sub-groups. (1845 : 395)

Darwin's own testimony clearly implies that only the specimens from Chatham and Charles were mingled together, since he was later able to compare these specimens as a group with the specimens collected on James Island.

David Lack's insistence that Darwin began to separate and label his specimens by locality after leaving Charles Island is, nevertheless, called into question by the seemingly inaccurate nature of several of the island localities actually recorded by Darwin. Indeed, Darwin's type specimens have provided a considerable nightmare of taxonomic problems for subsequent ornithologists, based largely on their controversial localities. Darwin claimed, for example, that specimens of a peculiarly large-beaked form of *Geospiza magnirostris* came from Chatham and Charles islands. But after more than a century of subsequent collecting without finding any such large-billed specimens, ornithologists found themselves faced with a puzzle. Either this form had become extinct on Chatham and Charles islands, where no *magnirostris* specimens (large or small) had ever been found by other expeditions; or else Darwin's specimens must have come from islands other than those indicated. Swarth (1931 : 147-49), noting that the largest bills among *G. magnirostris* are found in the northern part of the archipelago, including James Island, believed that Darwin's specimens came from that island. Although Darwin's specimens are still somewhat larger than the present James Island race of this species, Swarth concluded that some evolution in bill size must have occurred since Darwin's visit. Darwin also reported taking specimens of the smaller-billed *G. [magnirostris] strenua* on Chatham Island, and these specimens as well have generally been thought to have come from James Island (Fig. 3)⁶.

David Lack, who at first agreed with the judgment of Swarth and others⁷, later changed his mind, given Darwin's testimony that only the specimens from the first two islands had been mingled together. Yet Lack himself distrusted other of Darwin's localities, including some involving specimens from the one island—James—where Lack claimed Darwin had kept his specimens separate. According to Lack (1945 : 14), one of Darwin's specimens of *Cactornis scandens*, labelled as coming from James Island, is actually an example of *Geospiza difficilis* (now *nebulosa*), the Sharp-beaked Ground Finch, and belongs to a form that is not found on James Island today. So either measurable evolution has occurred in the size of the beak, or, more probably, the specimen came from Charles Island, where FitzRoy collected a very similar specimen of this now extinct island race. Altogether, there is serious doubt about the accuracy of eight of the fifteen localities recorded on Darwin's Geospizinae type specimens⁸.

Not only is the accuracy of Darwin's localities in doubt, but so is the means by which Darwin might have recorded this information. From his voyage specimen catalogues and other scientific notes it is very difficult to see how he could have supplied as much information as he later did in this regard. His *Ornithological Notes*, for example, lists localities for only three of his thirty-one Geospizinae, namely, for three specimens of a very distinctive species (*Camarhynchus psittacula*) that he recalled having seen on only one island—James. Moreover, this information was apparently recorded to indicate the rarity of the species rather than its locality per se. For the same reason Darwin also noted such information for two other Galapagos birds.

Darwin is known, of course, to have used FitzRoy's collections after the voyage to supplement his own record of localities. But this source of information still does not account for the localities entered on Darwin's own type specimens. Presumably, Darwin might have recorded localities on his specimen tags rather than in his catalogues. For this reason ornithologists have repeatedly bemoaned the fact that no original labels in Darwin's or John Gould's hand have ever been found among Darwin's type specimens at the British Museum. In the nineteenth century it was the custom of the museum curators to throw away the original collector's labels and to replace them with neatly printed museum labels. Information thought worthy of preserving was transferred to the new labels. But much valuable information, such as the original collector's numbers, was inevitably lost. George Robert Gray, who assisted Darwin with the *Birds* volume of the *Zoology of the Voyage of H.M.S. Beagle*, and who later received Darwin's types from the Zoological Society when it closed its museum, was a typical offender in this regard (Sharpe, 1906 : 84-85).



Fig. 3 Beagle type specimens of Darwin's finches. From top to bottom: *Geospiza magnirostris magnirostris*; *G. magnirostris strenua*; *G. fortis*; *G. nebulosa nebulosa*; and *Camarhynchus parvulus parvulus*. (Courtesy of the British Museum [Natural History], Sub-department of Ornithology, Tring.)

The question of whether or not Darwin recorded island localities directly on the specimen tags is largely resolved, however, by the fortunate discovery of one (and probably the only surviving) original label for his ornithological specimens. Having vainly sought, like previous investigators, for original labels among Darwin's type specimens, it occurred to me to examine all those Darwin specimens at the British Museum (Natural History) that are not endemic to the Galapagos. One such specimen was at last found (*Dolichonyx oryzivorus*—the American Bobolink), bearing what appears to be Darwin's original crude paper tag. Comparison of the specimen number (3374) with Darwin's manuscript catalogue shows that the number is indeed Darwin's, and that it is inscribed in his own hand (Fig. 4)⁹. On the reverse side of the tag the genus name, 'Dolichonyx', is written in pencil, in an unidentified hand, and below it, in ink, the species name, 'oryzivorus', appears, apparently in John Gould's hand. A second and smaller label, added when the specimen was presented to the Zoological Society in 1837, records Darwin's name, the date of accession, and, on the back, Darwin's original specimen number. The specimen was acquired by the British Museum in 1881, after Gould's death, along with many other birds from his huge personal collection. A third label (not shown) was attached to the specimen at this time.



Fig. 4 Darwin's specimen of *Dolichonyx oryzivorus*, with the only surviving label in Darwin's hand. (Courtesy of the British Museum [Natural History], Sub-department of Ornithology, Tring.)

Being a migrant species with an unusually wide range (from Canada to Chile), the Bobolink is an occasional visitor to the Galapagos in the autumn of each year. Coincidentally, in its autumn plumage the Bobolink is not unlike a Darwin's finch, although Darwin initially thought the bird was a pipit of very unusual structure¹⁰. When Gould first examined the bird in 1837, he thought it was a new species of finch. But he later discovered that it was an already described North American species and apparently decided to keep the specimen for his own collection¹¹. This circumstance, together with the lack of scientific importance of the specimen, enabled its original Darwin and Zoological Society labels to survive.

What is particularly important about this specimen, with regard to Darwin's labelling practices, is that no island locality is recorded on either of the two earliest tags. Darwin did consider this information worth recording in his *Ornithological Notes*, however, since the bird had been encountered on one island only—James. Thus it appears that whatever island localities Darwin thought worth recording, such as those for three finch and four mockingbird specimens, were recorded in the master catalogue of specimens and in the *Ornithological Notes* rather than on the crude paper tags¹².

In short, Darwin does not appear to have altered his collecting or labelling practices while he was in the Galapagos Archipelago. After he left Charles Island, his collecting procedures continued to reflect the typological and creationist assumptions he had brought with him to that archipelago. What localities he did record were noted as largely incidental information to remind himself later of scarce species or noteworthy habitats. He continued, moreover, to collect only a few specimens of each species; and he entirely failed to collect finches on the third island he visited—Albemarle—even though almost every finch within miles was gathered in front of him at a spring near Bank's Cove¹³. Darwin thereby passed up the chance of collecting an additional species, and two endemic subspecies, of Galapagos finches. Even after leaving James Island and setting sail for Tahiti, Darwin apparently continued to treat the vice-governor's comment about the tortoises, and his own discovery with regard to the mockingbirds, as isolated anomalies. For if he had fully appreciated the revolutionary implications of these facts, he would never have allowed his *Beagle* shipmates to devour and discard all thirty adult tortoises brought on board ship as a source of fresh meat for the cruise across the Pacific (FitzRoy, 1839 : 498)¹⁴.

These conclusions regarding Darwin's collecting procedures during his Galapagos visit bring us back once again to the problem of his finches and their dubious localities. In particular, if Darwin recorded only three island localities for these birds in his scientific notes, how and when did he derive the many additional localities that are now to be found on his type specimens? To answer this question I must take up the topic of what happened to Darwin and his finches after they returned from the *Beagle* voyage.

Darwin's return to England

After a voyage of nearly five years, the *Beagle* landed in Falmouth, England, on 2 October 1836. During the next several months Darwin arranged for the disposal and description of his collections within the various branches of natural history. His collection of birds and mammals, offered to the Zoological Society of London, was delivered on 4 January 1837¹⁵. The celebrated ornithologist John Gould, who was closely associated with the Zoological Society, lost no time in examining and naming the unusual finches that Darwin had brought back from the Galapagos Islands. At the very next meeting of the society (10 January), Gould described these birds as twelve new species, which he placed in one genus and two closely allied subgenera (*Geospiza*, *Cactornis*, and *Camarhynchus*). Moreover, he astutely realized the basic peculiarity of these finches, namely, that 'the bill appears to form only a secondary character'. Soon afterwards Gould recognized *Certhidea olivacea*, the Warbler Finch, as a thirteenth species of the group, belonging to yet another genus¹⁶.

Darwin, who was at this time residing in Cambridge, did not learn of the details of Gould's analysis until he moved to London in early March of 1837 in order to have closer contact with the specialists working on his collections. Gould's findings, communicated to Darwin during a meeting with the eminent ornithologist, provided Darwin with a number of surprises¹⁷. While in the Galapagos, Darwin had been rather unclear about the precise relationship among the various finchlike species he had encountered there. In particular, he had misidentified several finch species as the forms that they, through extensive evolutionary radiation, now appear to mimic. For example, he had considered the Cactus Finch, *Cactornis scandens*, to be a member of the Icteridae (the family of the orioles and blackbirds); and he had classified the Warbler Finch, *Certhidea olivacea*, as a 'wren', or warbler. It appears, moreover, that Darwin initially distinguished as separate species of finches only 6 of the eventual 13 forms that Gould named in early 1837. Hence Darwin's finches only really became Darwin's *finches* after Gould rectified many of Darwin's earlier field misclassifications, and thereby clarified the unity and complexity of the group¹⁸. More important still for Darwin's evolutionary thinking, Gould (1837*d*) declared that 3 of the 4 island forms of Galapagos mockingbird brought to England by Darwin were distinct species, a possibility that Darwin had already asserted 'would undermine the stability of

Species'. For the Galapagos as a whole, Gould pronounced 25 of the 26 land birds as new and distinct forms found nowhere else in the world. Darwin was frankly stunned, not only by the realization that three separate species of mockingbirds indeed inhabited the different islands of the Galapagos, but also by the fact that most of these Galapagos species, even though new, were closely related to those found on the American continent¹⁹. His conversion to the theory of evolution, which took place shortly after his meeting with Gould in March of 1837, was a direct consequence of these two conclusions.

Reconstructing the finch localities

In the wake of Gould's taxonomic findings, many of them quite unexpected, Darwin soon realized that the unusual features of the Galapagos finches could be largely explained if they, like the mockingbirds, were confined to separate islands. He therefore began to solicit information from those shipmates on the *Beagle* who had made their own private ornithological collections and who, unlike himself, had fortunately kept accurate records of the islands from which they had procured their specimens. Captain FitzRoy's extensive collection, which had gone to the British Museum on 21 February 1837, offered relatively easy access, and Darwin later acknowledged his use of it in the *Zoology* (1841 : 99)²⁰. What Darwin did not say in the *Zoology*, however, was that he also employed two other shipmates' collections, including that of his own servant, in attempting to reconstruct these island localities. The first of these sources of information came from Harry Fuller, who had spent a week collecting with Darwin on James Island. Altogether Fuller collected eight specimens of *Geospiza*, one from Chatham Island and seven from James. The collection of Darwin's servant, Syms Covington, was somewhat smaller and included only four finches, one from Chatham Island and three from Charles Island.

Records of Darwin's use of locality information from the collections of FitzRoy, Fuller, and Covington are among Darwin's manuscripts at Cambridge University Library (Figs. 5 & 6)²¹. There are four such sheets, in Darwin's hand. Although none of the sheets are dated, indirect evidence indicates that Darwin lost little time after he became an evolutionist in trying to reconstruct the Galapagos finch localities. One of the four sheets, which bears an 1836 watermark (manufacturer unknown), comprises a series of questions about Galapagos specimen localities evidently sent to FitzRoy and answered by an unidentified amanuensis or clerk (Fig. 5). On this same sheet an amanuensis, working for Darwin, also asked from what island of the Falklands a specimen of fox had come. Darwin mentioned the results of this latter inquiry in his *Journal of Researches* (1839 : 250–51), which was already in press by mid-August 1837. Similarly, Darwin's statement in his *Journal* (1839 : 475) that he 'very much suspect[ed]' that certain species of Galapagos finches were confined to separate islands corroborates the conclusion that he had already examined the various *Beagle* collections by the time his *Journal* went to press. Since Darwin had reached the Galapagos chapter of his *Journal* by late May or early June and since he had finished with the whole of the *Journal* by the end of June, his efforts to collate the various *Beagle* Geospizinae by locality probably date from June at the latest²².

It was undoubtedly at this time, that is, sometime in the spring or early summer of 1837, that Darwin also tried to reconstruct the island localities of his own Galapagos specimens. For a few birds Darwin was able to infer from his notes or from memory that he had collected these specimens on one island only. This was the case, for example, for an owl, a swallow, a flycatcher, and for three finch specimens with a peculiar beak shaped like that of a parrot (*Camarhynchus psittacula*). In addition, from his *Beagle* shipmates Darwin apparently acquired several finch specimens that were lacking in his own collection, and at least one of these had a locality attached²³.

Unfortunately, certain of Darwin's attempts to reconstruct the island localities of his own specimens involved a bit of guesswork, and errors inevitably crept in. In his master catalogue of specimens, for example, he drew a line under the first eight Geospizinae and wrote

What islands in the Galapagos do following birds
come from.

398	-	Chatham Is ^l Male	
399	-	6♀ " "	
400	-	6♀ " "	Female of 404
404	-	Charles's " "	In the skin of 400 heard
406	-	6♀ " "	Apten Trifurcatus
413	-	Female " "	Female (no head)
414	-	6♀ " "	Female - do
423	-	6♀ " "	Female - do
431	-	6♀ " "	Female - do

245 Fat. - From which island Past (Falklands)
Female.

Fig. 5 Darwin's request for information regarding the island localities of FitzRoy's Galapagos birds, with replies in the hand of an unidentified amanuensis. A second unidentified amanuensis, who is known to have worked for Darwin after the *Beagle* voyage, addressed the last question on the list, which was in turn answered by the first amanuensis. Additional memoranda, later added by Darwin, appear at the right of most of the entries. (Courtesy of the Syndics of Cambridge University Library.)

8

Birds from Galapagos Archipelago, etc.
 5 Lyons Covington, in papers of J. Lyton Esq.

Geospiza magnirostris, two specimens Charles I.^o
 ——— *fortis* ——— Charles I.^o
 ——— *fuliginosa* ——— Chatham I.^o

Do created 5 full in Capt. F.R. Maffin

392	}	<i>Geospiza magnirostris</i>	Charles I. Chatham I. ^o
417		—————	<i>straminea</i> James I. ^o
427	}	—————	<i>fortis</i> James I. ^o
422			do
434			do
433	}	<i>Geospiza parvula</i>	James I. ^o
432			
423		<i>Geospiza gutturalis</i>	James I. ^o

Fig. 6. Darwin's notes on the island localities of Covington's and Fuller's Galapagos finches. (Courtesy of the Syndics of Cambridge University Library.)

‘Chatham Is^d??’²⁴. The reason Darwin surrounded this locality designation with three question marks is evident from the order of the catalogue entries as a whole. As may be seen from the number sequence assigned to his birds, Darwin ticketed, numbered, and catalogued the entire collection only after leaving the Galapagos Archipelago in late October 1835. Within the list of birds, the entries proceed topsy-turvy, with specimens from the different islands entered in no apparent order²⁵. It is hardly surprising, then, that at least two of the eight specimens that Darwin later assigned to Chatham Island appear to have been mislabelled (see pages 63–64).

In the process of attempting to correlate the results from four different collections, Darwin inadvertently made other mistakes. In the *Zoology* (1841 : 101) he later gave the locality of *Geospiza fortis* as Charles and Chatham islands; but this was clearly an error, since the *Beagle* specimens all came from Charles and James²⁶. Further inaccuracies are associated with Darwin's claim about geographic representation among the various species of the Geospizinae. Eager to squeeze whatever evolutionary evidence he could from these finches, Darwin systematically collated the island localities of the four *Beagle* collections to see if any of the species represented one another on the different islands. In two genera, *Cactornis* and *Camarhynchus*, he claimed this to be the case. Of the numerous specimens shot by four collectors at James Island, he reported, all belonged to *Cactornis scandens* and *Camarhynchus psittacula*, whereas the specimens collected either on Chatham or Charles were those of *Cactornis assimilis* and *Camarhynchus crassirostris*. 'Hence we may feel almost sure', he concluded, 'that these islands possess their representative species of these two sub-groups' (1845 : 395).

Darwin's analysis of these two genera was plagued by several errors. In actual fact, FitzRoy had collected a specimen of *Cactornis assimilis* on James, not Charles or Chatham islands, thus invalidating half of Darwin's claim. Furthermore, Darwin had not collected long enough on any of these islands to realize that the various finch species are by no means confined to single islands. *Camarhynchus crassirostris*, for example, is found not only on Charles Island, where Darwin believed his own specimens had probably been taken, but also on Chatham and James. Similarly, *Cactornis scandens* and *Camarhynchus psittacula* are not confined to James Island, as Darwin had thought, but are found on the other islands he visited. Thus Darwin's claim about geographic representation in this group of four species is not only wrong in every detail, but it is not even substantiated by the *Beagle's* own collections. It is no wonder, then, that Darwin was so excited and relieved, in 1845, by Joseph Hooker's rigorous demonstration of representation in his several hundred species of Galapagos plants. To Hooker he wrote in July of that year, 'I cannot tell you how delighted and astonished I am at the results of your examination; how wonderfully they support my assertion on the differences in the animals of the different islands, about which I have always been fearful' (1887, 2 : 22). Darwin lost no time in adding Hooker's welcome results to his *Journal of Researches*, which he was then engaged in revising for the second edition²⁷.

Fortunately, the errors and uncertainties associated with Darwin's ornithological specimens did not affect the published results of the *Zoology of the Voyage of H.M.S. Beagle* that much. Of the seventeen localities that Darwin published for his finches, fifteen were either provided or corroborated by the other shipmates' collections. Darwin himself, employing an educated guess, was able to supply localities for two additional species that only he had collected. In the end only two species of finches remained without any locality whatsoever.

Unfortunately, what later ornithologists generally failed to appreciate was that Darwin's published localities were not necessarily those of his own specimens. In fact, the largely borrowed nature of Darwin's published localities for his Galapagos finches has had one curious repercussion that has confused even further the localities of the *Beagle* type specimens. A number of originally unlabelled Darwin specimens appear to have acquired island localities later in a completely circular fashion, based on the published information provided in the *Zoology of the Voyage of H.M.S. Beagle*. Curators at the British Museum apparently noticed that certain Galapagos species were indicated in the *Zoology* as coming from one island only. They therefore assumed that unlabelled Darwin specimens of these species must have come from those published localities. The specimens in question now carry these island localities on their labels; and in the British Museum's published list of type specimens there are notes to see the relevant pages of the *Zoology of the Voyage of H.M.S. Beagle*²⁸. In certain instances (for example, in the case of Darwin's specimens of *Otus galapagoensis*, *Hirundo concolor*, and *Dolichonyx oryzivorus*), these derivative localities are indeed correct, since Darwin was the only person on the *Beagle* to collect these species,

whose localities he was later able to recall. But this same process of circular relabelling is apparently what accounts for at least four of Darwin's finches being given localities that do not necessarily belong to them²⁹.

More ironically still, three of Captain FitzRoy's accurately labelled specimens have also suffered from this relabelling process, based once again on Darwin's published testimony. In one instance FitzRoy's specimen of *Camarhynchus psittacula*, which was procured on James Island, was relabelled as coming from Charles Island. This error was precipitated by the loss of Darwin's three type specimens of *C. crassirostris*. *C. crassirostris* and *C. psittacula* are somewhat similar species. FitzRoy's slightly aberrant specimen of *psittacula*, which was later thought to be the missing type of *crassirostris*, was accordingly reassigned to that species. But the island locality now had to be altered as well to agree with Darwin's dubious, but 'official', information for the type of *C. crassirostris*³⁰. The classification error was eventually caught by Swarth (1931 : 208), but the specimen in question still bears two island localities. Similarly, two other FitzRoy specimens, one being the type of *Geospiza nebulosa*, were also relabelled incorrectly, owing once again to Darwin's published localities³¹.

In short, the published designations of the *Zoology* were seen by later ornithologists and museum curators as more definitive than the accurately labelled FitzRoy specimens that had largely supplied this information. Swarth (1931 : 11) actually dismissed FitzRoy's localities wholesale, assuming his specimens could have come from practically anywhere in the archipelago³². David Lack (1945, 1947), although not going quite so far, assumed that all of FitzRoy's specimens were really Darwin's, and that those specimens labelled as coming from either Chatham or Charles Island could have come from either locality. With all of these confusions about the localities of Darwin's and FitzRoy's specimens, it is little wonder that the *Beagle* types have proved so problematical to ornithologists over the last hundred years.

Because there has been so much misinformation with regard to the various specimens of Geospizinae collected during the *Beagle* voyage, and because Darwin's published localities for these birds were largely derived from other *Beagle* collections, I have thought it worthwhile to present a brief history and description of all the known specimens. Altogether, there were between 56 and 58 Geospizinae collected by four different *Beagle* shipmates. Precise information regarding the collectors, the localities, and the sexes of many of these *Beagle* Geospizinae is provided here for the first time, based on hitherto unknown manuscript sources. In addition, I have supplied measurements of all the specimens (see the Appendix), and have reassigned several birds that appear to have been misclassified by Gould or later ornithologists. I shall begin with Darwin's collection, which was the largest.

Darwin's collection

Darwin collected 31 specimens of Geospizinae in the Galapagos Archipelago (1963 [1836] : 262-64). These, along with the rest of his ornithological specimens, were presented to the Zoological Society of London on 4 January 1837. Most of the specimens were subsequently mounted and displayed in the society's museum, as was customarily done with type specimens in the nineteenth century. In 1855 the Zoological Society decided to close its museum, and the British Museum was given first pick of the specimens (Sharpe, 1906 : 251). Unfortunately George Robert Gray, who was then the curator in charge of birds, did not acquire all the *Beagle* type specimens, a fact that has been greatly regretted by subsequent ornithologists. Of Darwin's 31 specimens of Geospizinae, only 19 were included among the 403 birds purchased from the Zoological Society on 19 December 1855. A few months later Darwin presented the British Museum with 3 additional Galapagos birds, including a specimen of finch ('*Geospiza*'). The following year John Gould sold 2 more of Darwin's '*Geospiza*' to the museum, bringing the total to 22³³. Three of these specimens appear to have been subsequently lost, so that the present total at the British Museum stands at 19 specimens (see note 84). None of these birds bear any indication of their sex on the old

nineteenth-century labels. Although this information is presented here for most of the specimens, it is derived from Sharpe's (1888) and Swarth's (1931) sometimes conflicting inferences from plumage. These designations cannot therefore be regarded as entirely accurate, except in the case of adult males.

Geospiza magnirostris Gould = *Geospiza magnirostris magnirostris* Gould³⁴

The British Museum has at least two Darwin specimens of this large-billed form of *magnirostris*. Specimen no. 1855.12.19.80 is an adult male and is labelled on its nineteenth-century tag as coming from 'Chatham Isl'. A newer red type specimen tag gives the locality as 'Chatham Is? [Charles Is.]'. The second specimen, no. 1855.12.19.113, is a female and is labelled as coming from 'Chatham'. Both of these specimens are undoubtedly among the eight that Darwin, after the voyage, guessed he had collected on 'Chatham Is^{d??}'³⁵. It is possible that the specimen tags at the Zoological Society originally carried question marks after the locality designation. Both specimens were subsequently mounted, and the locality on the stands was probably given without a question mark. When the specimens were taken off the stands in 1855 and provided with British Museum labels, the uncertainty of the original locality information was doubtless forgotten³⁶. The red type label on specimen no. 1855.12.19.80, which gives the locality as 'Chatham Is? [Charles Island]', dates from the early decades of this century, and reflects an attempt to second-guess the locality designation on the much older tag.

Geospiza strenua Gould = *Geospiza magnirostris strenua* Gould, *Geospiza fortis* Gould, and *Geospiza nebulosa debiliostris* Ridgway

There are four Darwin specimens of *Geospiza strenua* (*sensu* Gould) in the British Museum, an adult male (no. 1855.12.19.81) and three females (nos. 1855.12.19.83, 1855.12.19.114, and 1856.3.15.4). According to a note on the label of specimen no. 1855.12.19.83, Gould's (1841 : 101) description of the female of this species was taken from this individual. The specimen, which has a very small bill, was definitely not the bird figured by Gould in the *Zoology*. The male bears the locality 'Chatham Isl.' on its nineteenth-century tag and 'Chatham Island?' on the newer red type specimen tag. The first two females are indicated as coming from 'Chatham Isl.'. The other female specimen has no locality. The three specimens bearing a Chatham locality are undoubtedly among the eight that Darwin later assigned to 'Chatham Is^{d??}' in his master catalogue. If Darwin was correct about the locality of these three specimens, then two of them are extremely small examples of *G. magnirostris magnirostris*, which Fuller's collection conclusively establishes as the Chatham Island race of this species. On the other hand, the third and even smaller Chatham specimen (Gould's female type) must belong to a large example of *G. fortis*³⁷. According to David Lack (1947 : 23), the fourth bird is a typical specimen of *G. difficilis* [now *nebulosa*] *debiliostris* and hence must have come from James Island³⁸.

There is very good reason to question the Chatham Island localities ascribed to specimens no. 1855.12.19.81 and no. 1855.12.19.114. First of all, the presence of such diminutive examples of *G. magnirostris magnirostris* on the same island as the largest known example of this species (see under Fuller's collection), implies an extraordinary degree of variation in this island form. But even granting that the character range for *G. magnirostris magnirostris* was extremely great on Chatham Island, Darwin's two small examples depart from the mean size of culmen, bill depth, and wing length for this subspecies by an average of 3.8 and 3.5 standard deviations. Such disparities are significant at the .001 level³⁹. (For the sake of argument, I have made this statistical comparison using the largest standard deviation that has ever been observed in *G. magnirostris*, anywhere in the archipelago, for each of the three characters involved in the computation.) Moreover, using culmen length in specimen no. 1855.12.19.81 and wing length in specimen no. 1855.12.19.114, the probability that either of these two birds came from Chatham Island is less than one in ten thousand. The probability that *both* birds came from Chatham is virtually nil. What therefore seems quite

likely is that these two specimens are examples of *G. magnirostris strenua*, taken on James Island, where the subspecies overlaps with these specimens in all of their basic dimensions. In this connection, it should be remembered that Darwin's locality designations for these two specimens were retrospective guesses made almost two years after he had visited the Galapagos. That Darwin may have accurately remembered where he had collected specimens of *G. magnirostris magnirostris* is possible; but that he accurately distinguished the localities of all the specimens of the two *G. magnirostris* subspecies is more doubtful. Indeed, he probably grouped all the large-billed birds together when he entered them in his catalogue, just as he did with other clearly distinguishable finch species. This, in turn, must have made it even more difficult for Darwin, later, to differentiate the localities of his two *G. magnirostris* subspecies. Finally, it is highly unlikely that Fuller was the only person to collect *G. magnirostris strenua* on James Island, where Darwin did the bulk of his own collecting. Several specimens should also be present in Darwin's collection, and these two specimens, of dubious locality and extremely diminutive size, are therefore probably from James.

With regard to Darwin's apparent error about the locality of his two *G. magnirostris strenua* specimens, he may have been partially misled by Gould's misclassification of a FitzRoy specimen. FitzRoy's single Chatham Island specimen of '*G. strenua*' is either a very large example of *G. fortis* or, more probably, a hybrid between *G. fortis* and *G. magnirostris magnirostris* (see page 68). Hence no true specimens of *G. magnirostris strenua* were taken on Chatham Island.

If I am wrong about reassigning Darwin's two diminutive specimens of *G. strenua* to the James Island form of *G. magnirostris strenua*, then the possibility cannot be ignored that they, too, are hybrids between *G. magnirostris magnirostris* and *G. fortis* on Chatham Island. It is unlikely, however, that the *Beagle* collections would have included three hybrid specimens out of eight Chatham Island examples of *G. magnirostris* and *G. fortis*, so I am considerably more confident that Darwin's two specimens, given their dubious locality, belong to the James Island form of *G. magnirostris strenua*.

Geospiza fortis Gould

The British Museum possesses three Darwin specimens of *G. fortis*. Two of them, which were misclassified by Gould, are noticed separately under *Geospiza strenua* and *Geospiza dentiostriis*. The other, a female from 'Charles Isl.' (no. 1855.12.19.82), was correctly identified by Gould. I strongly suspect that this specimen was originally collected by someone other than Darwin, to whom it must later have been given. In his *Ornithological Notes* and specimen catalogue, Darwin did not record a Charles Island locality for any of his birds, although he did later state that his three specimens of *Camarhynchus crassirostris* may have come from that island. Unlike *C. crassirostris*, however, *G. fortis* is not easily differentiated from other similar species. It is therefore extremely unlikely that Darwin could have reconstructed this locality from memory, especially since he was unable to do so for another specimen of this species (see under *Geospiza dentiostriis*). Darwin's servant, on the other hand, did collect a specimen of *G. fortis* on Charles Island. Covington later gave or sold this specimen, along with three other *Geospizinae*, to Darwin's friend Thomas C. Eyton. All the Covington specimens, but his Charles Island *G. fortis*, eventually came into the possession of the British Museum in 1885. I believe that Darwin, who lacked a female of this species (*sensu* Gould), acquired this specimen from Eyton so that it could be described by Gould⁴⁰. If I am wrong about the history of this specimen, then the locality on the tag is almost certainly a later addition by someone other than Darwin. Given the specimen's measurements, it could have come from any of the three islands on which Darwin collected finches (Chatham, Charles, and James). A jet black male, figured by Gould in the *Zoology*, has been lost.

***Geospiza dentirostris* Gould = *Geospiza fortis* Gould**

The British Museum possesses one specimen (no. 1855.12.19.176) of this so-named form, which was the only example collected by Darwin. From dissection, Darwin thought it was a male, but Gould considered it a female on the basis of its plumage (Darwin, 1841 : 102). Darwin was unable to provide a locality for this specimen. Both Swarth (1931 : 153) and Lack (1945 : 12) have considered the bird to be an example of *G. fortis*. Given the diminutive size of this specimen, especially in bill depth, it almost certainly came from Charles Island.

***Geospiza dubia* Gould = *Geospiza fortis* Gould**

The only type specimen for this species, a female, is lost. It was evidently not received by the British Museum in 1855, since it appeared in small type in Gray's *Hand-List* (1870 : 88). Based on Gould's description, Swarth (1931 : 155–56) considered this form to be an example of *G. fortis*. Darwin listed the locality as Chatham Island, and the specimen was undoubtedly one of the eight that, after the voyage, he guessed had come from that island.

***Geospiza fuliginosa* Gould**

Two Darwin specimens of *G. fuliginosa* are in the British Museum (nos. 1855.12.19.44 and 1857.11.28.247). Both are adult males and are labelled as coming from Chatham Island. These are the last of the eight specimens that Darwin later assigned to 'Chatham Is^d??' in his master catalogue of specimens. Although the specimens could have come from any of the three islands on which Darwin collected finches (Chatham, Charles, and James), they approach most closely in their measurements the Chatham Island form of *G. fuliginosa*. The female specimen that Gould described in the *Zoology* (1841 : 102) is not in the British Museum collection.

***Geospiza parvula* Gould = *Camarhynchus parvulus parvulus* (Gould)**

There are two specimens of *G. parvula* collected by Darwin (no. 1855.12.19.167, a female; and no. 1855.12.19.194, an adult male). Both specimens were evidently the models for Gould's coloured plate (1841 : Plate 39). They were at one time labelled as coming from Chatham Island (Sharpe, 1888 : 4), but neither specimen belongs to the distinctive Chatham Island form (*salvini*) of *C. parvulus* (Swarth, 1931 : 229–31)⁴¹. This Chatham Island designation has therefore been questioned on the labels and 'James Island' written on them as well. In the *Zoology* (1841 : 102), Darwin listed only James Island as the locality of this species, a designation undoubtedly based on the three FitzRoy and two Fuller specimens that did come from that island. I do not believe that Darwin gave his own specimens any locality. Warren & Harrison (1971 : 420) give James Island as the locality of type specimen no. 1855.12.19.194, relying solely on the information given in the *Zoology*. Both specimens surely acquired this 'James' locality on their labels by the same circular process of reasoning. Nevertheless, measurements of bill depth and wing length support the correctness of this James Island designation.

***Cactornis scandens* Gould = *Geospiza scandens scandens* (Gould) and *Geospiza nebulosa nebulosa* Gould**

Darwin's specimens of *C. scandens* include an adult male (no. 1855.12.19.125), a female (no. 1855.12.19.20), and a third specimen noticed separately under *Cactornis assimilis*. The first two birds are labelled as coming from James Island, but this is almost certainly a later designation provided by reference to the *Zoology* (1841 : 104). Lack (1945 : 14–15) assigns specimen no. 1855.12.19.20 to *G. difficilis* (now *nebulosa*) and suggests that it belongs to the extinct form of this species that FitzRoy collected on Charles Island (see *Geospiza nebulosa*, under FitzRoy's collection). From Darwin's statement in the *Zoology* (1841 : 105) that he and two other collectors were daily looking out for jet black examples of the Cactus Finch, it seems likely that at least some of his specimens did come from James Island, where he,

Bynoe, and Fuller spent a week collecting together. As Lack notes in this connection, the adult male specimen has 'so small a bill that it almost certainly came from James' (1945 : 16).

Cactornis assimilis Gould = *Geospiza scandens rothschildi* Heller and Snodgrass
—a straggler?

Darwin collected one specimen of this form (no. 1855.12.19.15), which Sharpe (1888 : 18) considered an immature male but Swarth (1931 : 198) thought a female⁴². Darwin did not know from which island he had procured it. According to both Swarth (1931 : 198) and Lack (1945 : 16), Darwin's specimen agrees most closely with the Bindloe form (*rothschildi*) of *G. scandens*. FitzRoy's collection includes an almost identical specimen taken on James Island, however, and Darwin's specimen probably came from there as well. James Island is only forty miles from Bindloe, and stragglers, mostly juveniles, have frequently been reported over even longer distances (Lack, 1945 : 106)⁴³.

Camarhynchus crassirostris Gould = *Platyspiza crassirostris* (Gould)

Darwin collected three specimens, one male and two females, of *C. crassirostris*, but none of them were acquired by the British Museum in 1855. Darwin was unsure about which island of the Galapagos he collected these specimens on, but he guessed that it was probably Charles. Since *C. crassirostris* is common only in the transitional zone, Darwin would have had to have collected this species either on Charles or James, the only two islands where he visited this zone. It is possible that he remembered taking *C. crassirostris* and *C. psittacula* on different islands. In this case, Charles Island is indeed the most likely locality for his *C. crassirostris* specimens, since he encountered *C. psittacula* only on James.

Camarhynchus psittacula Gould = *Camarhynchus psittacula psittacula* Gould

Darwin collected three specimens of *C. psittacula* on James Island, two males and one female (1863[1836] : 263). Only one of them, a supposed female (no. 1855.12.19.22), is now in the British Museum. Another specimen, also thought to have been a female, was acquired but has been lost (no. 1855.12.19.12). Since Darwin collected only one female of this species, the surviving specimen may well be a juvenile male. It is doubtful if the museum ever received the third specimen, since it was not recorded by Sharpe (1888 : 17). Darwin's locality for these specimens may definitely be trusted, since he explicitly noted in his *Ornithological Notes* that he had seen this well-defined species on one island only.

Certhidea olivacea Gould = *Certhidea olivacea olivacea* Gould

Three specimens of the Warbler Finch are credited to Darwin at the British Museum (no. 1855.12.19.126, a male, which is labelled as having once been Darwin's no. 3340; and two specimens of unknown sex, no. 1855.12.19.127 and no. 1855.12.19.164). The bird with the distinctive cinnamon throat, as figured by Gould, is no longer among the specimens at the British Museum (Swarth, 1931 : 255). Darwin believed his specimens came from Chatham and James islands and that the species was 'certainly found at the latter [island]' (1841 : 106). *Certhidea olivacea* shows distinctive variations by island, and Swarth (1931 : 255) confidently assigns Darwin's three specimens to James Island⁴⁴.

In his *Ornithological Notes* Darwin recorded collecting only two specimens of *C. olivacea* (nos. 3310 and 3340). On the back of manuscript page 74 of these notes he wrote, 'A number lost at the [Zoological] Society belong to *Geospiza (certhidea) olivacea*'⁴⁵. Included among these lost specimens was probably the male in Gould's coloured plate. It would therefore seem that Darwin, after the voyage was over, acquired a minimum of one and perhaps two additional specimens of this species from other *Beagle* collections. The most likely source of such replacement specimens would have been the collections of Covington and Fuller, which are noticed separately.

Other Darwin specimens

The accessions catalogue for birds received by the British Museum records three specimens of Darwin's finches that I have been unable to locate⁴⁶. The first is a specimen of *Camarhynchus psittacula* (no. 1855.12.19.12) that was seen by Swarth (1931 : 215) but that has since been lost. The second specimen, a '*Geospiza*' (no. 1855.12.19.43), was included like the first in the purchase from the Zoological Society. The third specimen, also a '*Geospiza*' (no. 1857.11.28.248), was purchased from John Gould along with no. 1857.11.28.247, a specimen of *G. fuliginosa* that is in the collection. In the British Museum's record of accessions, this third specimen is marked as having been destroyed. Several other missing Darwin specimens may now be at the Leiden Rijksmuseum van Natuurlijke Historie, and these specimens are discussed separately under that collection.

FitzRoy's collection

The captain of H.M.S. *Beagle*, Robert FitzRoy, possessed considerable interest in several branches of natural history. It was at his instigation that a naturalist was invited to accompany the *Beagle* on its voyage around the world. Since Darwin, as a condition of his appointment, had insisted upon the right to dispose of his voyage collections as he wished, FitzRoy apparently decided to undertake his own separate zoological collection for the benefit of the British Museum. When he was unable to leave the ship, he encouraged other officers of the *Beagle* to procure specimens for him. This occurred, for example, in the Galapagos, where Benjamin Bynoe, the surgeon of the *Beagle*, spent a week collecting for the captain on James Island. Another officer of the *Beagle*, Edward H. Hellyer, actually drowned while attempting to procure a specimen for FitzRoy's collection⁴⁷.

A copy of FitzRoy's manuscript catalogue of specimens is now at Cambridge University Library among Charles Darwin's papers⁴⁸. This catalogue indicates that FitzRoy collected 447 zoological specimens during the *Beagle* voyage. Sixty of these (50 birds and 10 reptiles) were procured in the Galapagos Archipelago. Each Galapagos specimen was carefully dated and labelled by island. FitzRoy's catalogue also notes the sex and eye colour of each specimen, the latter being something Darwin generally did not record. At least 13, and perhaps as many as 26 of FitzRoy's 50 Galapagos birds, were collected by Harry Fuller, another *Beagle* shipmate. After the voyage, most of Fuller's specimens were separated from FitzRoy's collection and were subsequently acquired by the Haslar Museum in Plymouth. This portion of FitzRoy's collection is noticed separately.

The ornithological portion of FitzRoy's catalogue lists the following specimen numbers and localities for the Galapagos Islands: nos. 387–400 (Chatham Island), nos. 401–10 (Charles Island), and nos. 413–38 (James Island). To the feet of each specimen was originally attached a tiny paper tag (roughly 4.5 mm × 12 mm) recording one of these assigned numbers. Only Fuller's specimens have retained these tiny tags. When the British Museum received the bulk of FitzRoy's collection on 21 February 1837, all of his specimens were given new numbers. Fortunately the old numbers were recorded in the museum's register of accessions, along with the island locality of each bird⁴⁹. There is accordingly no room for doubt about the island localities of any of FitzRoy's specimens at the British Museum. Later ornithologists, however, have rarely been aware of this fact.

Of FitzRoy's 50 Galapagos birds, only 24, including 13 *Geospizinae*, were presented to the British Museum. Fourteen of these specimens, including 8 *Geospizinae*, were evidently collected by Benjamin Bynoe⁵⁰. Of the remaining 26 Galapagos birds in FitzRoy's collection, at least 8 were *Geospizinae* that later went to the Haslar Museum. These specimens are noticed separately under Fuller's collection. Hence 18 of FitzRoy's specimens still remain unaccounted for. Most of them were probably Fuller's, since Darwin commented in his *Ornithological Notes* (1963[1836] : 265) that Fuller possessed several wading birds that his own collection lacked. It is also possible that some of these missing specimens were collected by other *Beagle* shipmates who, like Fuller, may have taken charge of them after the *Beagle*'s

return to England. Officers and ordinary seamen were under no obligation to collect for either FitzRoy or Darwin, and they were accordingly free to keep and sell in England whatever they procured. FitzRoy later reminded Darwin of this fact when he concluded, after seeing a draft of Darwin's acknowledgments section for the *Journal of Researches*, that Darwin had not given sufficient credit to the officers of the *Beagle* for assisting him in his collections⁵¹. Inasmuch as the officers generally made an effort to insure that Darwin and FitzRoy each received rare specimens, whatever these officers might have kept were undoubtedly duplicates or already described species⁵².

***Geospiza magnirostris* Gould = *Geospiza magnirostris magnirostris* Gould**

FitzRoy procured three specimens of this large-billed form of *magnirostris*, a female (no. 1837.2.21.398 = FitzRoy no. 403), an adult male (no. 1837.2.21.402 = FitzRoy no. 407), and a juvenile male (no. 1837.2.21.403 = FitzRoy no. 408). Sharpe (1888 : 8) gives the sex of this third specimen incorrectly. FitzRoy recorded that all three specimens were taken between 25 and 27 September 1835 on Charles Island, which should put an end to the many disputes about the locality of this form⁵³. It has generally been thought that this form became extinct on Charles Island in the nineteenth century. In 1957, however, Robert Bowman collected on Charles Island an adult female of *G. magnirostris* that he claimed overlapped with some of the *Beagle* specimens. Other birds of this species were also observed by Bowman at this time (1961 : 271). No one has seen or collected specimens of *G. magnirostris* on Charles Island since Bowman's visit. In all likelihood, the specimens seen by him in 1957 were part of a small population that had recently recolonized Charles Island from the north and that subsequently became extinct. This supposition is supported, moreover, by the measurements of Bowman's specimen, which are: culmen from nostril, 15.7 mm; bill depth, 19.6 mm; and wing, 77 mm (University of California, Berkeley, Museum of Vertebrate Zoology, specimen no. 140985). There is no overlap between these measurements and any of the large-billed *Beagle* specimens of *G. magnirostris magnirostris* taken on Charles Island. Bowman's specimen is, in fact, a typical example of *G. magnirostris strenua*, and it accords most closely with the smaller forms of this subspecies found in the centre of the archipelago. Since 1888 there have been two other reports of isolated specimens of *G. magnirostris* taken on Charles Island⁵⁴. Among Darwin's finches, colonizations of islands within the Galapagos group probably occur much more frequently than has hitherto been appreciated on the basis of collectors' evidence.

***Geospiza strenua* Gould = *Geospiza magnirostris magnirostris* Gould × *Geospiza fortis* Gould?**

FitzRoy collected one specimen of *G. strenua*, an adult male from Chatham Island (no. 1837.2.21.396 = FitzRoy no. 397). This specimen is intermediate between *G. magnirostris magnirostris* and *G. fortis* on Chatham Island. The measurements of the specimen are slightly larger than for any known race of *G. fortis*. They are also within the range of the smaller forms of *G. magnirostris*, but not of the larger forms of that species⁵⁵. Since the specimen is an adult male, and since its placement within the *G. magnirostris* group would require a variability in the exceptionally large Chatham Island race that would be fifty per cent greater than for any known form, the most reasonable assignment is to *G. fortis*. More plausible still is that the specimen is a hybrid between the two species. Hybrids are known to occur between these two forms in one or two per cent of all matings (Peter Grant, personal communication)⁵⁶.

***Geospiza fuliginosa* Gould**

FitzRoy's collection included three specimens of *G. fuliginosa*, a male (no. 1837.2.21.417 = FitzRoy no. 436) and two females (1837.2.21.410 = FitzRoy no. 420; and

1837.2.21.411 = FitzRoy no. 421). They were all procured on James Island. The first of these three specimens is missing at the British Museum (Natural History) and has evidently been lost or destroyed. Darwin recorded in his manuscript notes on FitzRoy's collection that the two female specimens belonged to *G. parvula*, and this was apparently Gould's own designation⁵⁷. As Swarth (1931 : 229) points out, the name *parvula* has commonly been applied to small examples of *G. fuliginosa*. In Gould's day it was not realized that males of *Camarhynchus parvulus*, unlike those of *G. fuliginosa*, are never fully black, and this circumstance added to the difficulty of distinguishing these two species.

***Geospiza nebulosa* Gould = *Geospiza nebulosa nebulosa* Gould**

Gould gave the name *G. nebulosa* to at least two specimens, of which one, a female, was collected by FitzRoy on Charles Island (no. 1837.2.21.400 = FitzRoy no. 405). A male specimen, which provided the type description, came from Darwin's collection and has unfortunately been lost. Swarth (1931 : 153) synonymized FitzRoy's specimen with *G. fortis*, but the specimen has much too narrow and pointed a bill to accord with that species. Lack (1945 : 14–15), on the other hand, placed the specimen with the *G. difficilis* group and, following Swarth (1931 : 190), thought that one of Darwin's specimens of *Cactornis scandens* (no. 1855.12.19.20) should also be reassigned to this form. The bills of these two specimens are slightly larger than in any known forms of *G. difficilis*, and both specimens lack the chestnut on the wing bar and undertail coverts, as is found in some members of the *G. difficilis* group⁵⁸. The only other species with which these two specimens exhibit even a slight overlap in measurements is *G. fortis*, which has, however, a larger average depth of bill than culmen, as measured from the nostril (Lack, 1947 : 174–76). In *G. difficilis*, as in the two *Beagle* specimens, the opposite is true. Moreover, *G. difficilis* and the two *Beagle* specimens possess a relatively straight culmen, whereas the culmen is definitely curved in the other species of *Geospiza*. Hence these two *Beagle* specimens agree most closely with the measurements and general characteristics of *G. difficilis*, and evidently constitute, as Lack himself concluded, an extinct race of this species from Charles Island.

Lack's opinion is reinforced by certain facts regarding the distribution of this species. *G. difficilis* is confined to the humid zone of those islands, like Charles, where *G. fuliginosa* is also present. Both Darwin and FitzRoy visited the highlands on Charles Island, and FitzRoy's specimen was shot on 27 September 1835, during the afternoon that Darwin and several *Beagle* officers made an excursion to the highest point on the island. Two specimens of the Galapagos Rail, which is also confined to the highlands, were procured for FitzRoy's collection during this same excursion. Another almost identical specimen of '*G. nebulosa*' was taken on Charles Island in 1852 by an expedition that also visited the highlands⁵⁹. Although once found on all of the larger islands in the archipelago, *G. difficilis* has definitely become extinct on several of them, probably owing to ground clearing and cultivation in the humid zone. It is hardly surprising, then, that *G. difficilis* may have encountered this same fate on Charles Island, which was the first island to be settled, in 1832. Within just a few years, ecological disturbances associated with the settlement were already manifesting themselves. Darwin (1963[1836] : 264) specifically noted that the larger species of ground finches, which normally prefer the arid lowlands, were extremely common on Charles Island near the cleared tracts at the highlands settlement. Indeed, these ground finches had become quite troublesome to the settlers, eating seeds buried up to six inches in the cultivated fields. Thus, by the mid-1830s any endemic Charles Island population of *G. difficilis* would have been faced with two threats to its continued existence: a diminishing habitat and increased competition from other species of Darwin's finches that are normally restricted to the lower altitudes. Although the reasons for their disappearance are less clear, two other species of birds, *Geospiza magnirostris* and *Nesomimus trifasciatus*, became extinct on Charles Island during the nineteenth century.

Other ornithologists have generally accepted Lack's judgment that FitzRoy's specimen of *G. nebulosa* is an extinct form of *G. difficilis* (Bowman, 1961 : 270; Harris, 1974 : 36).

Although the name *nebulosa* has not been used for nearly a century, the law of priority in nomenclature insists that the name of the first described subspecies shall have precedence over all later described subspecies of the same species. Thus the name *nebulosa* should technically replace *difficilis*, which was first proposed by Sharpe (1888 : 12) for the Abingdon Island race of this species. Lack (1945 : 14–15) recognized the need for this substitution but was reluctant to institute it because he thought, erroneously, that Gould's *G. nebulosa* was known from only two specimens whose localities were not entirely certain. The type locality, however, is now definitely established as Charles Island. Gould, moreover, apparently had a third—and now lost—specimen in his possession when he described this species. Finally, a fourth specimen was collected on Charles Island in 1852. Based on these facts, together with the subsequent agreement of ornithologists that Gould correctly differentiated FitzRoy's specimen of *G. difficilis* as *G. nebulosa*, the name *nebulosa* appears to have legitimate priority over *difficilis* (cf. Paynter, 1970 : 162). The following names therefore have priority for this species: *G. nebulosa nebulosa* Gould (the extinct Charles Island form of the species); *G. nebulosa difficilis* Sharpe (Abingdon and Tower islands); *G. nebulosa debiliostris* Ridgway (Narborough, James, and Indefatigable islands); and *G. nebulosa septentrionalis* Rothschild and Hartert (Wenman and Culpepper islands).

The question of why the Charles Island subspecies of *G. nebulosa* possessed such a large bill can perhaps be answered, albeit somewhat speculatively, by considering the other finch species with which it would have been in competition for food resources. With the large average beak size of the ground finches on Charles Island, where *G. magnirostris magnirostris* was apparently the commonest bird in the lowlands, and with unusually small-billed tree finches in the highlands, the large bill of *G. nebulosa nebulosa* might plausibly be accounted for by the simultaneous operation of character release and character displacement in an upward direction. Indeed, Charles Island is unique in being the only island in the Galapagos on which the majority of resident Geospizinae have smaller bills than *G. nebulosa*. Hence a net upward displacement in bill size would be expected compared with other subspecies of this species.

***Geospiza parvula* Gould = *Geospiza fuliginosa* Gould and *Camarhynchus parvulus parvulus* (Gould)**

FitzRoy collected three specimens of *G. parvula* (*sensu* Gould) on James Island. Two of these specimens have been correctly reassigned to *G. fuliginosa* by subsequent ornithologists and are separately noticed under that species. The third specimen, a female, is a valid example of *C. parvulus* (no. 1837.2.21.414 = FitzRoy no. 428). No specimen with this registration number actually exists at the British Museum. But there are two specimens bearing reg. no. 1837.2.21.411; and one of these, a female of *C. parvulus*, is evidently the missing specimen.

***Cactornis scandens* Gould = *Geospiza scandens scandens* (Gould)**

FitzRoy collected one example of *C. scandens*, an adult male, on James Island (no. 1837.2.21.412 = FitzRoy no. 424). This specimen was the jet black one shot by Bynoe and mentioned by Darwin in the *Zoology* (1841 : 105). The specimen is missing from the British Museum collection.

***Cactornis assimilis* Gould = *Geospiza scandens rothschildi* Heller and Snodgrass
—a straggler?**

FitzRoy's collection included a single juvenile male specimen of this form, which was procured on James Island (no. 1837.2.21.415 = FitzRoy no. 430). Both Sharpe (1888 : 18) and Swarth (1931 : 198) give the sex incorrectly. For the identity of this specimen, see *Cactornis scandens*, under Darwin's collection.

***Camarhynchus psittacula* Gould = *Camarhynchus psittacula psittacula* Gould**

There is a single individual of *C. psittacula* in FitzRoy's collection, a male that was procured on James Island (no. 1837.2.21.413 = FitzRoy no. 426). According to Darwin (1963[1836]: 264), this specimen was shot by Bynoe. The bird was originally designated *psittacula* by Gould, but it subsequently became confused with the type of *C. crassirostris*, acquiring that name and a Charles Island locality on the tag. Both Swarth (1931: 208) and Lack (1945: 16–17) concur that the specimen indeed belongs to *C. psittacula*, although it is perhaps slightly aberrant⁶⁰.

***Certhidea olivacea* Gould = *Certhidea olivacea olivacea* Gould**

FitzRoy's collection included one specimen of *C. olivacea*, a female collected on James Island (no. 1837.2.21.408 = FitzRoy no. 416).

Fuller's collection

Harry Fuller, FitzRoy's personal steward on the *Beagle*, collected eight specimens of Geospizinae while in the Galapagos Archipelago⁶¹. These birds now reside at the University Museum of Zoology, Cambridge, England. The specimens may be identified as Fuller's by the tiny numbered tags, corresponding to FitzRoy's *Beagle* catalogue sequence, that still adhere to the feet⁶². Fuller spent a week collecting with Darwin, Bynoe, and Covington on James Island, and seven of his eight specimens came from that island.

Information on a later set of specimen tags allows us to reconstruct the following history for Fuller's birds. Seven of his eight specimens have the name 'Dr. Armstrong' on the labels. This is apparently the same Dr Armstrong mentioned by John Stevens Henslow, during the *Beagle* voyage, in an 1834 letter to Darwin⁶³. Armstrong was in charge of the Haslar Museum (part of the Haslar Royal Naval Hospital in Plymouth), to which Fuller's specimens were either given or sold sometime after the *Beagle* voyage. In deciding whether Fuller had the right to dispose of his own specimens as he wished, it is relevant to note that the specimens that went to the Haslar Museum were not just duplicates but included some forms that FitzRoy's collection otherwise lacked. Given this fact, and given that only Fuller's specimens (and not Bynoe's) were subsequently withheld from the British Museum, it seems justified to speak of 'Fuller's collection' as a separate entity from FitzRoy's own official collection, to which Bynoe contributed⁶⁴.

In 1856, the Haslar Museum was closed down and its specimens were distributed to other museums and collections. In this connection, the Lords of the Admiralty presented a number of Haslar Museum mammals, birds, reptiles, fish, and molluscs to the British Museum on 12 January 1856⁶⁵. None of the birds given to the British Museum included Galapagos specimens. On the other hand, at least seven Galapagos birds (Armstrong's finches) were acquired by Sir William Jardine, in whose hand the later specimen tags are written. Jardine's tags indicate that the specimens were procured on the voyage of the *Beagle*, but no name other than Dr Armstrong's appears on the labels. After Jardine died, his collection of 8542 ornithological specimens was sold by auction in 1886. His seven Geospizinae were purchased by Alfred Newton, who deposited them in the University Museum of Zoology, Cambridge. There is an auctioneer's catalogue of Jardine's collection (Anonymous, 1886).

The eighth Cambridge specimen (FitzRoy no. 433) has a different history. It was at one time owned by Hugh Edwin Strickland, an ornithologist and friend of Darwin's. The earliest specimen tag indicates that the specimen was 'Procured by C. Darwin Esq.'. Strickland may have acquired the bird through Darwin, which would account for its erroneous ascription to him. Darwin in turn must have obtained the specimen from FitzRoy or Fuller. Strickland's collection of 6006 skins was given by his widow to the University Museum of Zoology, Cambridge, in 1867. A catalogue of Strickland's collection was later prepared by Salvin (1882).

Because these eight specimens were apparently named by Gould and were later used by Darwin in supplying locality information for the *Zoology*, they may be considered syntypes. None of the specimens possess island localities on their labels, and most are lacking an indication of the sex. This information has been resupplied here, based on Darwin's manuscript notes and FitzRoy's catalogue.

***Geospiza magnirostris* Gould = *Geospiza magnirostris magnirostris* Gould**

Fuller collected one specimen of this large-billed form of *magnirostris*, an adult male, on Chatham Island (no. 27/Fri[E]/26/e/2 = FitzRoy no. 392). Measurements of the bill exceed even the largest of the specimens procured by other *Beagle* collectors⁶⁶. Fuller's specimen establishes that the large-billed form of *magnirostris* was once endemic to two islands in the Galapagos—Charles, where FitzRoy and Covington collected it; and Chatham, where Darwin guessed he had taken two other specimens (see page 63). Thus Darwin may have accurately recollected taking specimens on Chatham Island. The species is now extinct on that island.

***Geospiza strenua* Gould = *Geospiza magnirostris strenua* Gould**

Fuller collected one specimen of this *G. magnirostris* subspecies, an adult male procured on James Island (no. 27/Fri[E]/26/e/1 = FitzRoy no. 417)⁶⁷.

***Geospiza fortis* Gould**

Fuller's collection includes three specimens of *G. fortis*, all collected on James Island (no. 27/Fri[E]/26/b/2 = FitzRoy no. 427, an adult male; no. 27/Fri[E]/26/b/3 = FitzRoy no. 434, also an adult male; and no. 27/Fri[E]/26/b/4 = FitzRoy no. 422, a female). Although Gould's original designation for these specimens was *G. fortis*, Jardine was evidently at a loss as to how to characterize them. On the labels he therefore entered only the genus name. Subsequently he inserted *nebulosa* as the species name, and later this name was synonymized with *difficilis* on the tags. Measurements establish that the specimens are all clearly examples of *G. fortis*.

***Geospiza parvula* Gould = *Geospiza fuliginosa* Gould**

Fuller procured two specimens of *G. parvula* (*sensu* Gould) from James Island (no. 27/Fri[E]/26/d/3 = FitzRoy no. 432, and later Jardine's specimen; and no. 27/Fri[E]/26/d/4 = FitzRoy no. 433, the specimen later acquired by Strickland). Both specimens are actually adult males of *G. fuliginosa* in black plumage and were incorrectly assigned by Gould⁶⁸. Jardine also assigned his specimen to *G. parvula*, the name that appears on his tag. In addition to the indication provided by their telltale plumage, measurements of the specimens also support their reassignment to *G. fuliginosa*.

Fuller claimed that specimen no. 432 was a female. Darwin alluded to this fact in the *Zoology*, since he was much puzzled by the collection of a female in black plumage and rightly considered the case exceptional (1841 : 99). The specimen in question is almost certainly an adult male, incorrectly sexed by Fuller.

***Camarhynchus psittacula* Gould = *Camarhynchus psittacula psittacula* Gould**

Fuller collected one specimen of *C. psittacula*, a male in juvenile plumage, on James Island (no. 27/Fri[E]/11/f/1 = FitzRoy no. 423). This specimen was previously thought to be a female, but FitzRoy's catalogue lists it as a male.

Covington's collection

Syms Covington, 'Fiddler and boy to Poop cabin' on the *Beagle*, became Darwin's servant and amanuensis during the second year of the voyage⁶⁹. Darwin taught him how to shoot and

skin birds, and Covington became a valuable assistant in all his collecting activities. How Covington came to have his own collection of birds from the Galapagos is something of a mystery, since he was employed to collect for Darwin. But he evidently possessed four Geospizinae and several other birds from the Galapagos that were not recorded as part of Darwin's own catalogue of specimens⁷⁰. Soon after the voyage the Geospizinae and at least two other Galapagos birds became the property of Thomas C. Eyton, a naturalist and close friend of Darwin's⁷¹. Covington was fortunately later able to tell Darwin from which islands his finch specimens were procured, and Darwin subsequently made use of this information when collating the localities of all the *Beagle* specimens for the *Zoology* (see page 58 & Fig. 6).

After Thomas Eyton died in 1880, a portion of his ornithological collection was purchased by the British Museum. Included in this purchase of 205 skins in 1881 were 2 birds from the Galapagos, a mockingbird and a dove. Both birds are now credited to Darwin, but they were almost certainly collected by Covington⁷². Covington's Galapagos finches had a different history. After Eyton's death, 3 of the 4 specimens passed into the hands of Osbert Salvin and Frederick Godman, both of whom had a keen interest in Galapagos birds. In 1885 Salvin and Godman presented these 3 specimens, along with 51 other Geospizinae from the collections of Dr Habel and Commander A. H. Markham, to the British Museum⁷³. There the 3 Covington specimens were erroneously presumed to be Darwin's, whose own name still appears on the labels. It is my belief that Covington's fourth finch is also in the British Museum collection, having been acquired and transmitted by Darwin at a much earlier date. Covington's specimens, which were undoubtedly seen by Gould, may be considered syntypes.

Geospiza magnirostris Gould = *Geospiza magnirostris magnirostris* Gould

Covington collected two specimens of this large-billed form of *magnirostris* (no. 1885.12.14.280, an adult male; and no. 1885.12.14.281, apparently a female). No island localities are given for these specimens, but Darwin recorded in his manuscript notes that Covington's specimens both came from Charles Island, where FitzRoy collected similar specimens.

Geospiza fortis Gould

At least one specimen of *G. fortis* was collected by Covington, on Charles Island. I strongly suspect that this specimen is no. 1855.12.19.82 at the British Museum, referred to separately under Darwin's collection. Darwin, who lacked a female of this species (*sensu* Gould), apparently borrowed it from Thomas C. Eyton in order that Gould might describe it (see page 64).

Geospiza fuliginosa Gould

Covington collected one specimen of *G. fuliginosa*, a female or juvenile male, on Chatham Island (no. 1885.12.14.320). The locality is given on the label.

The Leiden Rijksmuseum collection

Swarth (1931 : 12) has claimed that several Galapagos birds that he judged to be from the *Beagle* voyage, although he was not able to ascertain their history, exist at the Leiden Rijksmuseum van Natuurlijke Historie. There are seven possible *Beagle* specimens at the Leiden Rijksmuseum, including five Geospizinae. The Geospizinae were all purchased in 1863 from the well-known Amsterdam natural history dealer Gustav Adolph Frank. They include three specimens of *Geospiza fuliginosa* (one male and two females), a female of *Geospiza crassirostris* (= *Platyspiza crassirostris*), and a female of *Cactornis scandens* (= *G. scandens*). The other two Galapagos specimens are a male and a female of *Zenaida*

galapagoensis. These last two specimens once possessed labels written in the hand of Coenraad Jacob Temminck, a director of the Rijksmuseum, who died in 1858. Hence the two doves arrived at the Leiden Rijksmuseum even before the five Galapagos finches.

There is good reason to believe that most of these Leiden specimens are indeed *Beagle* (and Darwin) specimens. The British Museum (Natural History) is missing Darwin type specimens in all four of the categories represented in Leiden. These missing specimens include one female and probably more specimens of *Geospiza fuliginosa*⁷⁴, a specimen of *Cactornis scandens*, all three type specimens of *Camarhynchus crassirostris* (a male and two females), and the male type of *Zenaida galapagoensis*. Gould's measurements for this last specimen agree very closely with male specimen in Leiden. In addition, one of the two female specimens of *G. fuliginosa* in Leiden matches the description of the female type given in the *Zoology* (1841 : 101).

Were it not for two inconsistencies between these missing Darwin specimens and those in Leiden, I would feel sure that they are the same. First, Darwin collected only one specimen of the Galapagos Dove, not two, as are present in Leiden. Nevertheless other *Beagle* shipmates, in particular Darwin's servant, undoubtedly collected additional specimens of this common species. This may account for the presence of the second specimen in the Leiden collection. The second inconsistency concerns the sex of Darwin's missing specimen of *C. scandens*, which appears to be a male, not a female⁷⁵. But even if it is a male (and this is not certain), Darwin's missing specimen would be in a state of juvenile and hence 'female' plumage, so the possibility exists that the specimen in Leiden has been incorrectly sexed. According to Gerlof F. Mees, the sexes of the Leiden specimens were not originally entered on the labels but were later supplied around 1900 by estimation from the plumage⁷⁶. It is also possible that Swarth's (1931 : 190) 'female' specimen of *C. scandens* at the British Museum is actually a juvenile male. In this case the missing Darwin specimen would have to be a female, in agreement with the estimated sex of the specimen in Leiden. In this connection it must be emphasized that none of Darwin's specimens at the British Museum carry the sex on their labels. Doubtless the Zoological Society specimens lacked this information as well. Moreover, it is very common for females and juvenile males of Darwin's finches to be confused when the original collector's designation of the sex is missing⁷⁷. Measurements of the Leiden specimen of *C. scandens*, which has a small bill, establish that it came either from Chatham or, more probably, from James Island (in which case it must be a juvenile male). Both of these islands were visited by Darwin.

If the Leiden specimens are not Darwin's, the question arises as to who else might have collected them. It is virtually impossible that any of the Geospizinae in Leiden were collected by members of the *Beagle* voyage other than Darwin. He went to considerable trouble to track down all the other Geospizinae after the *Beagle* voyage, and all of these specimens are accounted for⁷⁸. Additionally, Darwin was the only person on the *Beagle* to collect specimens of *C. crassirostris*, a species that was never received by the British Museum but that is present in Leiden.

The question arises, therefore, as to who else visited the Galapagos between 1835, when the *Beagle* made the first systematic collections, and 1863, when the Leiden Rijksmuseum acquired its five Geospizinae. The first collection after Darwin's visit was made in 1838 by Adolphe-Simon Nébox, surgeon of the French frigate *Vénus*. Nébox's collecting was done on one island only, Charles, where the *Vénus* spent eleven days⁷⁹. Nébox collected specimens of the dove (*Zenaida galapagoensis*), swallow (*Progne modesta*), Medium Ground Finch (*Geospiza fortis*), and Cactus Finch (*G. scandens*), but he did not collect any other finches⁸⁰. Nébox's specimens are now at the Museum d'Histoire Naturelle in Paris, where they were presented in 1839 (Prévost & des Murs, 1855 : 204-9; Swarth, 1931 : 102). Another *Vénus* officer, the assistant surgeon Charles-René-Augustin Léclancher, procured four specimens of the Galapagos Dove, one female specimen of the Cactus Finch, and one specimen of an unidentified species of *Camarhynchus*⁸¹. Léclancher's specimens were described by Lafresnaye (1840, 1843), who kept three of the doves and the one specimen of *Camarhynchus* for his own collection⁸². In 1865, two years after the Leiden

Rijksmuseum acquired its own Galapagos finches, Lafresnaye's entire collection, including all of his Galapagos specimens, was sold to the Boston Society of Natural History. The collection now resides at the Museum of Comparative Zoology, Harvard University. None of the Galapagos finches have survived. I have been unable to trace the whereabouts of L  clancher's fourth dove and his one specimen of the Cactus Finch.

There were two other expeditions to the Galapagos after 1838 and before 1863. The first was that of H.M.S. *Herald*, which visited the islands in January 1846 but spent only seven days there. Stops were made at Chatham, Charles, and James islands. The naturalist on board was Thomas Edmonston, who met with a tragic end shortly afterwards (Seemann, 1853, 1: 67-69). Two specimens of Geospizinae, apparently collected by Edmonston, were later presented to the British Museum by Captain Henry Kellett and Lieutenant Wood of the *Herald* (Sharpe, 1888 : 11, 17).

The Galapagos Archipelago was visited again in May 1852 by the Swedish frigate *Eugenie*, which spent nine days there and visited Chatham, Charles, Indefatigable, Albermarle, and James islands. Dr Kinberg, the zoologist and surgeon of the expedition, collected 26 species of birds, including specimens of *Geospiza fuliginosa*, *G. nebulosa*, *G. scandens*, and *Zenaida galapagoensis* (Sundevall, 1871). He did not, however, collect specimens of *Platyspiza crassirostris*. Sundevall explicitly states that Kinberg provided an island locality for every specimen, but none of the specimens in Leiden possess this information. Moreover, Sundevall must have had the Kinberg collection in his possession after 1863 in order to write his later report. The birds from the *Eugenie* voyage are now at the Naturhistoriska Riksmuseet in Stockholm (Swarth, 1931 : 33).

What is noteworthy about all of these other expeditions to the Galapagos is that none of them reported collecting specimens of *P. crassirostris*, which lives in the transitional and humid zones and would not normally be collected by someone on a brief visit. Darwin is the only person known to have collected this species until the *Albatross* expedition procured specimens in 1888. Moreover, the Leiden specimen of *P. crassirostris*, which has a very small depth of bill, appears to have come from Charles Island, where Darwin reported taking his own specimens. All in all, Darwin's collection therefore remains the most likely source for the specimens in Leiden.

If the Leiden specimens are Darwin's, they may have been acquired by Gustav Adolph Frank, and then by the Leiden Rijksmuseum, through the agency of John Gould. Gould at one time owned at least four Galapagos specimens collected by Darwin, and these he probably acquired in 1855 at the dispersal of the Zoological Society's Museum. Gould was a shrewd dealer in specimens, always on the lookout for birds that could be sold or exchanged to his advantage. It is said that for many years not a hummingbird arrived in London without Gould getting to it first. Between 1857 and 1860 he sold three of Darwin's Galapagos specimens, including two Geospizinae, to the British Museum⁸³. That Gould, during this same period, may have traded other Darwin specimens that eventually found their way to Leiden is certainly plausible. Of additional relevance is the fact that Gould maintained a lively correspondence with Temminck, the Leiden Rijksmuseum director, and exchanged numerous specimens with him over the years (Mees, 1964, 1967). The two Leiden specimens of *Zenaida galapagoensis*, which were acquired independently of the finches and prior to Temminck's death, may therefore have come directly from Gould.

Appendix: Specifications concerning the *Beagle* collections of Geospizinae

The Table that follows presents a summary of measurements and other relevant information concerning the *Beagle* collections of Darwin's finches. In my measurements I have attempted to duplicate David Lack's (1945 : 76) procedures in order to facilitate comparison between the *Beagle* type specimens and Lack's extensive tables of measurements for each

island population (1945 : 142–51; 1947 : 168–85). All bill measurements were made with either vernier or dial calipers accurate to better than 0.1 mm, a distance that is smaller than the normal range of error involved in duplicating these measurements. (The use of dividers is not recommended for fine measurements of this sort, since dividers, owing to their angular divergence, tend to overestimate distances.)

The culmen was measured from the anterior lip of the nostril to the tip of the bill. Insertion of calipers any distance into the nostril results in a larger and more variable measure, so all measurements were taken from just inside the most superficial portion of the nostril lip. There is occasionally some bilateral asymmetry in the culmen (from nostril) distance. All measurements given here were therefore taken from the right side of the specimen, as viewed from the dorsal side. For depth of bill, calipers were positioned to yield the largest possible measure between the base of the bottom mandible and the top of the upper mandible. This point on the upper mandible is usually not where the mandible meets the feathered skull, but rather somewhat anterior to this spot, before the curved culmen begins to descend. All bill measurements were taken six times. The high and the low measurements were then discarded, and the four remaining measurements averaged. Wing measurements were taken of both wings, when present, using a millimeter rule. The flattened wing was measured from the carpal joint to the tip of the longest primary, to the nearest 0.5 mm.

These various measurements are presented in the Table that follows, along with the name of the person who collected the specimen, the specimen's institutional location and registration number, its specific and subspecific identity, its sex, and the island from which it was procured. Under the heading *Form*, the correct classification is given first and is followed by the name on the label(s). Under the heading *Island*, the locality given on the label(s) is presented first, in quotation marks, and is separated from the real, or most probable, locality by a colon. Where an island name alone follows the colon, the locality provided is accurately established by manuscript evidence. Where the colon is followed by the expression '—form of subspecies' (indicating a particular island), the locality has been estimated on the basis of the specimen's measurements and plumage, which coincide with only one possible island form, given the various islands known to have been visited by the collector.

The Table includes all existing specimens, as well as the 5 British Museum (Natural History) specimens that have been lost or destroyed since 1837. Not included in the Table, except insofar as they may be represented among the 2 missing '*Geospiza*' listed on page 80 or among the Leiden Rijksmuseum collection, are 10 specimens already described under Darwin's collection that are not at the British Museum. These, in summary, seem to be: one adult male specimen of *Geospiza fortis*, one female specimen of *G. dubia*, one female specimen of *G. fuliginosa*, one male specimen of *G. nebulosa*, one juvenile male specimen of *Cactornis scandens*, one male and two female specimens of *Camarhynchus crassirostris*, one male specimen of *C. psittacula*, and one male specimen of *Certhidea olivacea*. All in all, at least 27 and possibly all 31 of Darwin's Geospizinae are accounted for as currently present at the British Museum (Natural History) and the Leiden Rijksmuseum, or as having been lost or destroyed since 1837⁸⁴. Similarly, of the 25 to 27 specimens procured by other *Beagle* collectors, all but 2, both of which were among the 13 FitzRoy specimens that went to the British Museum in 1837, appear to have survived.

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Table: Specifications concerning the *Beagle* collections of Geospizinae*

Collector	Specimen	Form	Culmen	Bill Depth	Wing		Sex	Island
					Left	Right		
Darwin	BM(NH) 1855.12.19.80	<i>Geospiza magnirostris magnirostris</i> (= 'G. magnirostris')	17.7	21.8	90	90.5	ad. ♂	'Chatham?' and 'Charles': probably Chatham
Darwin	BM(NH) 1855.12.19.113	<i>G. magnirostris magnirostris</i> (= 'G. magnirostris')	17.7	21.7	—	87.5	♀(?)	'Chatham': probably Chatham
FitzRoy	BM(NH) 1837.2.21.398	<i>G. magnirostris magnirostris</i> (= 'G. magnirostris')	17.1	22.1	85	85.5	♀	'Charles': Charles
FitzRoy	BM(NH) 1837.2.21.402	<i>G. magnirostris magnirostris</i> (= 'G. magnirostris')	18.9	22.3	90	91	ad. ♂	'Charles': Charles
FitzRoy	BM(NH) 1837.2.21.403	<i>G. magnirostris magnirostris</i> (= 'G. magnirostris')	17.2	22.2	88	86	juv. ♂	'Charles': Charles
Fuller	UMZC 27/Fri(E)/26/e/2	<i>G. magnirostris magnirostris</i> (= 'G. magnirostris')	18.2	23.8	91	92	ad. ♂	'Galapagos': Chatham
Covington	BM(NH) 1885.12.14.280	<i>G. magnirostris magnirostris</i> (= 'G. magnirostris')	18.3	22.5	93	90.5	ad. ♂	'Galapagos': Charles
Covington	BM(NH) 1885.12.14.281	<i>G. magnirostris magnirostris</i> (= 'G. magnirostris')	18.5	21.7	87.5	84	♀(?)	'Galapagos': Charles
Darwin	BM(NH) 1855.12.19.81	<i>G. magnirostris strenua</i> (= 'G. strenua')	13.9	17.8	79.5	79	ad. ♂	'Chatham?': James form of subspecies
Darwin	BM(NH) 1855.12.19.114	<i>G. magnirostris strenua</i> (= 'G. strenua')	15.7	18.1	73.5	74.5	♀(?)	'Chatham': James form of subspecies
Fuller	UMZC 27/Fri(E)/26/e/1	<i>G. magnirostris strenua</i> (= 'G. magnirostris')	14.7	18.5	83	84	ad. ♂	'Galapagos': James
FitzRoy	BM(NH) 1837.2.21.396	<i>G. magnirostris magnirostris</i> × <i>G. fortis</i> ? (= 'G. sirenuia')	14.3	16.0	82.5	81.5	ad. ♂	'Chatham': Chatham
Darwin or Covington	BM(NH) 1855.12.19.82	<i>G. fortis</i> (= 'G. fortis')	12.5	13.2	71	71	♀(?)	'Charles': Charles?
Darwin	BM(NH) 1855.12.19.83	<i>G. fortis</i> (= 'G. strenua')	14.0	14.8	75	74	♀(?)	'Chatham': probably Chatham
Darwin	BM(NH) 1855.12.19.176	<i>G. fortis</i> (= 'G. dentirostris')	10.3	10.1	—	67	juv. ♂ (?)	'Galapagos': Charles form of species

* All measurements are in millimetres.

Collector	Specimen	Form	Culmen	Depth	Bill	Wing	Right	Sex	Island
Fuller	UMZC 27/Fri(E)/26/b/2	<i>G. fortis</i> (= ' <i>G. difficilis</i> ')	12.1	13.4	73	72		ad. ♂	'Galapagos': James
Fuller	UMZC 27/Fri(E)/26/b/3	<i>G. fortis</i> (= ' <i>G. difficilis</i> ')	12.2	12.1	67.5	68.5		ad. ♂	'Galapagos': James
Fuller	UMZC 27/Fri(E)/26/b/4	<i>G. fortis</i> (= ' <i>G. difficilis</i> ')	12.2	12.6	—	67		♀	'Galapagos': James
Darwin	BM(NH) 1855.12.19.44	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	8.9	8.1	61.5	62.5		♀ (?)	'Chatham': probably Chatham
Darwin	BM(NH) 1857.11.28.247	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	8.8	8.2	64.5	65		♀ (?)	'Chatham': probably Chatham
Darwin?	LRNH Cat. 2, pur. 1863	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	8.5	8.0	66	65		ad. ♂	'Galapagos': locality uncertain
Darwin?	LRNH Cat. 3, pur. 1863	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	8.7	7.5	63.5	63		♀ (?)	'Galapagos': locality uncertain
Darwin?	LRNH Cat. 4, pur. 1863	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	8.5	7.6	62	62		♀ (?)	'Galapagos': locality uncertain
FitzRoy	BM(NH) 1837.2.21.410	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	8.0	7.1	58	60		♀	'James': James
FitzRoy	BM(NH) 1837.2.21.411	<i>G. fuliginosa</i> (= ' <i>G. parvula</i> ')	8.4	8.0	61	60		♀	'James': James
FitzRoy	[i.e., 1837.2.21.414] BM(NH) 1837.2.21.417	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	Missing					♂	'James': James
Fuller	UMZC 27/Fri(E)/26/d/3	<i>G. fuliginosa</i> (= ' <i>G. parvula</i> ')	8.5	8.0	65	—		ad. ♂	'Galapagos': James
Fuller	UMZC 27/Fri(E)/26/d/4	<i>G. fuliginosa</i> (= ' <i>G. parvula</i> ')	8.0	8.1	64	65		ad. ♂	'Galapagos': James
Covington	BM(NH) 1885.12.14.320	<i>G. fuliginosa</i> (= ' <i>G. fuliginosa</i> ')	9.4	8.5	62	62		♀ (?)	'Chatham': Chatham
Darwin	BM(NH) 1855.12.19.20	<i>G. nebulosa nebulosa</i> (= ' <i>C. scandens</i> ')	11.0	10.4	71	72		♀ (?)	'James': extinct Charles subspecies
FitzRoy	BM(NH) 1837.2.21.400	<i>G. nebulosa nebulosa</i> (= ' <i>G. nebulosa</i> ')	10.8	10.2	71	72		♀	'Chatham' and 'Charles': Charles
Darwin	BM(NH) 1856.3.15.4	<i>G. nebulosa debilirostris</i> (= ' <i>G. strenua</i> ')	9.6	8.6	67	66.5		♀ (?)	'Galapagos': James form of subspecies

Darwin	BM(NH) 1855.12.19.125	<i>G. scandens scandens</i> (= ' <i>C. scandens</i> ')	12.3	8.5	66	68	ad. ♂	'James': James form of subspecies
Darwin?	LRNH Cat. 1, pur. 1863	<i>G. scandens scandens</i> (= ' <i>C. scandens</i> ')	11.6†	9.2	69	69	juv. ♂ (?)	'Galapagos': probably James form of species
FitzRoy	BM(NH) 1837.2.21.412	<i>G. scandens scandens</i> (= ' <i>C. scandens</i> ')	Missing				ad. ♂	'James': James
Darwin	BM(NH) 1855.12.19.15	<i>G. scandens rothschildi?</i> (= ' <i>C. assimilis</i> ')	14.4	10.1	72.5	71.5	juv. ♂ (?)	'Galapagos': probably James
FitzRoy	BM(NH) 1837.2.21.415	<i>G. scandens rothschildi?</i> (= ' <i>C. assimilis</i> ')	14.1	10.2	70.5	70.5	juv. ♂	'James': James
Darwin?	LRNH Cat. 2, pur. 1863	<i>Platypiza crassirostris</i> (= ' <i>G. crassirostris</i> ')	10.5	11.6	87	86.5	juv. ♂ (?)	'Galapagos': probably Charles form of species
Darwin	BM(NH) 1855.12.19.12	<i>Camarhynchus psittacula psittacula</i> (= ' <i>C. psittacula</i> ')	Seen by Swarth (1931 : 215); now missing.				♀ (?)	'James': James
Darwin	BM(NH) 1855.12.19.22	<i>C. psittacula psittacula</i> (= ' <i>C. psittacula</i> ')	10.5	11.2	72.5	69.5	♀ (?)	'James': James
FitzRoy	BM(NH) 1837.2.21.413	<i>C. psittacula psittacula</i> (= ' <i>C. psittacula</i> ')	10.4	12.5	79	78	♂	'Charles' and 'James': James
Fuller	UMZC 27/Fri(Ey)11/f/1	<i>C. psittacula psittacula</i> (= ' <i>C. psittacula</i> ')	10.1	10.4	70	72	juv. ♂	'Galapagos': James
Darwin	BM(NH) 1855.12.19.167	<i>C. parvulus parvulus</i> (= ' <i>G. parvula</i> ')	7.0	6.5	59.5	60	♀ (?)	'Chatham' and 'James': James form of subspecies
Darwin	BM(NH) 1855.12.19.194	<i>C. parvulus parvulus</i> (= ' <i>G. parvula</i> ')	4.9†	6.6	60	61.5	ad. ♂	'Chatham' and 'James?': James form of subspecies
FitzRoy	BM(NH) 1837.2.21.411	<i>C. parvulus parvulus</i> (= ' <i>G. parvula</i> ')	6.5	7.2	58.5	59	♀	'James': James
Darwin	BM(NH) 1855.12.19.126	<i>Certhidea olivacea olivacea</i> (= ' <i>C. olivacea</i> ')	7.3	5.0	56	55	♂	'Galapagos': James form of subspecies

†Denotes a broken culmen.

Collector	Specimen	Form	Culmen	Bill		Wing		Sex	Island
				Depth	Left	Right	Left		
Darwin?	BM(NH) 1855.12.19.127	<i>C. olivacea olivacea</i> (= ' <i>C. olivacea</i> ')	7.8	4.4	53.5	56.5	?	'Galapagos': James form of subspecies	
Darwin?	BM(NH) 1855.12.19.164	<i>C. olivacea olivacea</i> (= ' <i>C. olivacea</i> ')	6.0†	4.7	53.5	53	?	'Galapagos': James form of subspecies	
FitzRoy	BM(NH) 1837.2.21.408	<i>C. olivacea olivacea</i> (= ' <i>C. olivacea</i> ')	7.5	4.3	54.5	53.5	♀	'James': James	
Darwin	BM(NH) 1855.12.19.43	' <i>Geospiza</i> '	Missing					Unknown	
Darwin	BM(NH) 1857.11.28.248	' <i>Geospiza</i> '	Destroyed					Unknown	

† Denotes a broken culmen.

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Notes

1. Darwin's finches have been the subject of numerous systematic treatments, of which the most important are by Gould (1837a, 1841, 1843), Salvin (1876), Ridgway (1890, 1897), Rothschild & Hartert (1899, 1902), Snodgrass & Heller (1904), Swarth (1931), Hellmayr (1938 : 130–46), Lack (1945, 1947, 1969), Bowman (1961, 1963), Paynter (1970 : 160–68), Harris (1974), and Steadman (in press). Monographic works, such as those by Swarth (1931) and Lack (1945, 1947), have usually given Darwin's finches family or subfamily status—the latter being the general consensus. Nevertheless, some authors have recommended that they be accorded only tribal status within the Emberizinae subfamily (Paynter & Storer, 1970 : vii). Differentiation between subfamilies and tribes is a subjective matter, and I have preferred to follow the monographic tradition on this point. Species and genus names of certain forms of the Geospizinae have changed over the years, making for some minor inconsistencies in terminology in discussions of the literature. For example, *Cactornis scandens* (Gould, 1837a) is no longer given separate generic status, but is classified instead with the other species of *Geospiza*. I have followed the policy of using the original names proposed by Gould (1837a, 1841) when discussing individual *Beagle* specimens or Darwin's views about them. Otherwise, the current nomenclature has been followed, with the exception that I recognize *Geospiza magnirostris magnirostris* and *G. magnirostris strenua* as valid trinomials and also recognize the name *G. nebulosa* as having priority over *G. difficilis*. See pages 69–70 and note 53.

2. According to FitzRoy (1839 : 490), Lawson came on board the *Beagle* on 25 September and then escorted a party, including Darwin and FitzRoy, to the settlement in the highlands. Darwin spent four days on Charles Island, the last being 27 September. See also Darwin's *Diary* (1933 : 336).

3. DAR 31.2: MS p. 342v (all DAR numbers refer to the Darwin MSS, Cambridge University Library): 'The Thenca of Albermale [*sic*] Island is the same as that of Chatham Is^d—'. Contrary to Darwin's voyage opinion, the mockingbirds from Albemarle (*Nesomimus parvulus*) and Chatham (*N. melanotis*) are now recognized as separate species by some ornithologists, whereas the James and Albemarle forms are both assigned to *N. parvulus*. Gould (1841 : 62–63), to confuse matters further, later synonymized the Chatham and James forms under the name *melanotis*, which merely goes to show that the Chatham, Albemarle, and James forms are all very similar in appearance and would be classified by many ornithologists as subspecies. The Charles Island form of the mockingbird (*N. trifasciatus*) is more noticeably distinct, but even this form would be ranked as a subspecies by some ornithologists. See Harris, 1974 : 128; and Davis & Miller, 1960 : 447–48.

4. DAR 31.2: MS pp. 341–42.

5. Toward the end of the voyage Darwin prepared a series of separate specimen catalogues for the use of the specialists who later took charge of his collections after the *Beagle*'s return to England. The *Ornithological Notes* (1963[1836]) constitutes one of twelve such catalogues. On the dating of these catalogues, see Sulloway (1982b).

6. See, for example, Rothschild & Hartert, 1899 : 155; Swarth, 1931 : 149; and Lack, 1945 : 9. Similarly, Hellmayr has concluded: 'There seems hardly any doubt that in the case of *G. strenua* and *G. magnirostris* the localities, as given . . . in the "Zoology of the Beagle", are altogether untrustworthy' (1938 : 130, n.3). As recently as 1973, Ian Abbott reached a similar conclusion (6 December 1973 letter to the British Museum [Natural History], Sub-department of Ornithology, Tring, excerpted on a typed sheet stored with the *Beagle*

collections of *G. magnirostris*). Abbott believed these specimens were probably collected on Abingdon or Tower Island, which were briefly visited by some *Beagle* officers and crew.

7. See Lack, 1940 : 49; and 1945 : 9–10.

8. These doubtful localities involve the following birds: two specimens of *Geospiza magnirostris* (British Museum registry nos. 1855.12.19.80 and 1855.12.19.113, labelled as coming from Chatham Island but thought to have come from James); two specimens of *G. parvula* (British Museum nos. 1855.12.19.167 and 1855.12.19.194, labelled as coming from Chatham Island but elsewhere assigned to James [Darwin, 1841 : 102]); one specimen of *Cactornis scandens* (British Museum no. 1855.12.19.20, labelled as coming from James but assigned by Lack to an extinct race of *G. difficilis* [now *nebulosa*] on Charles or Chatham Island); and three specimens of *G. strenua* (British Museum nos. 1855.12.19.81, 1855.12.19.83, and 1855.12.19.114, labelled as coming from Chatham but thought to have come from James).

9. In addition, the paper is similar to that used by Darwin on the *Beagle* voyage. The registry number of this specimen at the British Museum is 1881.5.1.2394.

10. In his *Ornithological Notes* he wrote: 'Anthus. was shot by Fuller on James Isd: it was the only one specimen seen during our whole residence. It is described as rising from the ground suddenly & again settling on the ground—Showed in its flight long wings, like a Lark; uttered a peculiar cry.—Its structure appear[s] very interesting' (1963[1836] : 265).

11. Whether Gould acquired the specimen in 1837, or whether he perhaps acquired it as late as 1855, when the Zoological Society closed its museum and sold all its ornithological specimens, is not known. Gould also possessed other Darwin type specimens. In 1857 he sold 251 ornithological specimens to the British Museum, including 2 specimens of *Geospiza* that once belonged to Darwin (reg. nos. 1857.11.28.247 and 1857.11.28.248). See 'Zoological Accessions Aves, 1854–1873', p. 64, and 'Zoological Accessions Aves, 1880–1884', p. 106; British Museum (Natural History), Sub-department of Ornithology, Tring.

12. This conclusion is confirmed by an analysis of the locality information published by Waterhouse (1845) in his paper on Darwin's Galapagos insects. Of 29 species, 14 have island localities and 15 do not. Each of these 14 localities is recorded as well in Darwin's specimen catalogue; and the island and habitat information given by Waterhouse corresponds exactly to Darwin's own wording in that catalogue. Thus only where this information was recorded in Darwin's notes was it preserved for later use. Darwin apparently recorded such information incidentally as part of the habitat description. For example, specimens 3363 and 3364 are followed by the comment: 'Small insects, sweeping; high up, central parts of Charles Island' ('Printed Numbers 3345[–3907]', Down House). In his section on advice to collectors, which appeared only in the first edition of his *Journal of Researches* (1839 : 598–99), Darwin recommended that a number be placed on each specimen immediately after it was procured, and that this number be entered in the specimen catalogue 'during the very same minute' so that the locality would never be subject to doubt. If localities had been recorded on the numbered tags, this precaution would have been unnecessary. Finally, that none of Darwin's ornithological specimens had localities on the labels is reinforced by Gould's failure to provide any island designations for the Galapagos species he named in January and February of 1837. See 'Zoological Society of London. Minutes of Scientific Meetings Oct. 1835 to Aug. 1840', pp. 120–21, 123–24, 129–30, 134; and Gould, 1837*a, b, c, d*.

13. In his *Diary*, Darwin wrote in this connection: 'To our disappointment the little pits in the Sandstone contained scarcely a Gallon [of water] & that not good. It was however sufficient to draw together all the little birds in the country; Doves & Finches swarmed round its margin' (1933 : 338; entry for 1 October 1835). Similarly, FitzRoy commented: 'Around this scanty spring draining continually through the rock, all the little birds of the island appeared to be collected, a pretty clear indication of there being then no other fresh-water within their reach . . .' (1839 : 495).

14. These tortoises, from Chatham Island, were brought on board the *Beagle* just five days

before Darwin returned from James Island. FitzRoy had earlier embarked eighteen Chatham Island tortoises, and these were devoured as well. FitzRoy did, however, bring two Hood Island tortoises back to England ('Zoological Accessions, 1837', p. 1; British Museum [Natural History], Mammals Library, London). Two other very small tortoises also survived the *Beagle* voyage—apparently brought home as pets (DAR 29.3 : 40, MS p. 7v). When Darwin finally realized the significance of having an expert taxonomist decide whether the reported differences between the tortoises were of specific distinction, these four tortoises were the only ones available. Although they were from three different islands (Hood, Charles, and James), they were all too young to be of value (Darwin, 1839 : 465). Darwin also missed an opportunity to bring back an adult carapace of the unusual saddleback form of tortoise on Charles Island. According to FitzRoy (1839 : 492), numerous shells were lying around at the Charles Island settlement, where they were being used as flower pots. Within about ten years of Darwin's visit, the Charles Island tortoise was extinct. Zoologists had to wait nearly a century to find remains of this form in a lava cave (Broom, 1929).

15. Several of his specimens, including his Bobolink, still bear this date of accession on the labels. It seems likely that Darwin presented the specimens in person since he came to London from Cambridge that same day to deliver a paper before the Geological Society (Darwin, 1837*a*). He also wrote a letter dated 4 January that was read that afternoon at a meeting of the Zoological Society Council. According to the minutes of that meeting, Darwin's letter 'announced a present to the Society of his entire Collection of Mammalia and Birds made during His Majesty's Surveying Vessel *Beagle*. It was ordered that the best thanks of the Society be returned to Mr. Darwin for his liberal and valuable contribution to its preserved Collections: and that his wishes with respect to the disposal of the duplicate specimens in this Collection, and to the mounting and describing of the same be strictly complied with' (unpublished 'Zoological Society Minutes of Council', 5: 79–80).

16. See 'Zoological Society of London. Minutes of Scientific Meetings Oct. 1835 to Aug. 1840', p. 120; manuscript record of the meeting of 10 January 1837. For the number of finch species named by Gould on 10 January 1837, see Sulloway, 1982*a* & 1982*b*. On 10 May Gould again brought Darwin's finches before the Zoological Society, naming 14 species in 4 genera, including *Certhidea olivacea* (see 'Minutes', pp. 164–65). Gould's fourteenth species, *Geospiza incerta*, lived up to its name, for he subsequently synonymized it under one of the others. A curious remnant of this change of mind remains in the published *Proceedings of the Zoological Society*, for although it is said that 14 species were named, only 13 names and descriptions follow (Gould, 1837*a*). Also of interest is the fact that the published *Proceedings* lists under the 10 January 1837 meeting the names and descriptions that were only given later by Gould at the 10 May meeting. Thus the published record, by transferring the events of 10 May back to 10 January and by deleting the earlier presentation, obscures the difficulties that Darwin's finches caused even such a celebrated ornithologist as John Gould.

17. For further details about Darwin's meeting with Gould, and evidence that they had not discussed the Galapagos specimens before this time, see Sulloway (1982*b*).

18. For further information see Sulloway, 1982*a*. Gould's 13 species are not identical, however, with the present 13 species of Galapagos finches. Contrary to the legend, Darwin collected only 9 of these 13 species. Four of Gould's species—*Geospiza strenua* (= *Geospiza magnirostris strenua* and *G. fortis*), *G. dentirostris* and *G. dubia* (= *G. fortis*), and *Cactornis assimilis* (= *G. scandens*)—have proved to be only slightly variant forms of 3 other species. Given the relative paucity of material with which he had to work, Gould's confusion is nevertheless understandable. The 4 species of Galapagos finches that Darwin did not collect are *Geospiza conirostris* (the Large Cactus Finch), *Camarhynchus pallidus* (the Woodpecker Finch), *C. heliobates* (the Mangrove Finch), and *C. pauper* (the Medium Tree Finch). These species were all procured by later expeditions between 1868 and 1899. The sole Cocos Island member of the Geospizinae (*Pinaroloxias inornata*) was collected in 1840 during the voyage of H.M.S. *Sulphur* and was described by Gould (1843).

19. It is often claimed that Darwin was impressed by the American character of his Galapagos finches (see, for example, Silverstein, 1974 : 505; and Ruse, 1979 : 164). But

Darwin's finches played no role in this aspect of his evolutionary insight. Rather it was the mockingbirds, the flycatchers, the dove, and numerous other typically American species that established this generalization about the Galapagos avifauna. The finches, in contrast, were placed with the Fringillidae in the nineteenth century, and this family of birds was then believed to be worldwide. It is only in this century that the Fringillidae and Emberizidae, under which Darwin's finches are now classified, have been distinguished as families of Old and New World finchlike species, respectively. Although Darwin's finches have no close ancestor on the American continent today, some ornithologists believe they arose from a form related to the emberizine genus *Volatinia* (and several similar genera). These species are all seed-eating ground birds that range from southern United States to northern Chile and Argentina (Paynter & Storer, 1970 : vii). Relying on osteological and other evidence, Steadman (in press) has argued that the Geospizinae evolved from *Volatinia jacarina*, the Blue-black Grassquit. He also contends that the Cocos Island Finch and the Galapagos finches were established by two independent invasions of this species from Central and South America, respectively.

20. For the date of FitzRoy's presentation of specimens, which included 187 skins, see the manuscript catalogue 'Zoological Accessions Aves, 1837-1851-3', pp. 7-15; British Museum (Natural History), Sub-department of Ornithology, Tring. FitzRoy presented one further specimen on 15 March 1837, an egg of *Rhea darwinii*. FitzRoy's Galapagos portion of the collection included 50 skins, 21 of them finches, all with an island locality. Some of these Galapagos specimens belonged to another shipmate, however; and only 24 Galapagos skins, 13 of them finches, actually went to the British Museum.

21. See DAR 29.3 : 26, 28-30. Ironically, that other shipmates on the *Beagle*, but not Darwin, recorded island localities for their birds marks Darwin as the only real scientist aboard that ship. For Darwin collected with a theory, however mistaken, in mind. The other shipmates were mere collectors, and their labelling practices reflect that fact.

22. That Darwin's manuscript notes on this question were initially compiled in connection with the writing of his *Journal* is reinforced by another consideration. On the list of Covington's and Fuller's birds, which occupies one of the four sheets, Darwin mistakenly referred *Camarhynchus psittacula* to the genus *Geospiza* (see Fig. 6). He also misspelled *psittacula* as *spittacula*. This same species name is misspelled and assigned to the genus *Geospiza* in a list of Galapagos species that Darwin compiled in the spring of 1837 during a meeting with John Gould (Sulloway, 1982*b*). Darwin was not, therefore, entirely familiar in the spring of 1837 with the generic or specific names that Gould had just given these species. The use of erroneous generic and specific names on the locality list for Covington's and Fuller's birds suggests that these notes too were compiled about this time. The name *psittacula* was altered to *psittaculus* in the *Zoology* (1841 : 103), so these notes on Covington's and Fuller's specimens clearly predate that change. I would assign Darwin's two other sheets of notes on his Galapagos finch localities to late 1840, when he was working on the final instalment of the ornithological portion of the *Zoology*. One sheet, which records all thirteen of FitzRoy's finch localities, may be dated by the use of the specific name *Camar[hjy]nchus] psittaculus*. The other, although it bears the name *psittacula*, is probably of the same date, since it contains a collated list of localities for all the *Beagle* collections as published in the *Zoology* (1841 : 100-106).

23. See pp. 64, 66, 71, and 73.

24. See 'Printed Numbers 3345[-3907]', Down House, under specimen nos. 3312-19. The catalogue is written in ink. The line under the first eight specimens and the comment 'Chatham Is^d??' were added later in pencil, almost certainly after Darwin's return to England.

25. Of those specimens for which island localities are listed (eighteen) or were later published by Darwin (two), or for which localities can be reconstructed on the basis of other evidence (nine), the sequence runs: James (3299); James (3303); James (3304); Charles (3306); Chatham (3307); Chatham (3308); Charles or James (3309); James (3310); the eight specimens of finch that Darwin later assigned to Chatham with three question marks

(3312–19); James (3330–32); James (3340); Charles or James (3342–44); Chatham (3345); Albemarle (3349); James (3350); James (3356); James (3362); and James (3374). I have deduced seven of these twenty-nine localities from information unknown to Darwin. *Certhidea olivacea* exhibits distinctive characteristics by island, and Darwin's specimens (3310 and 3340) definitely belong to the James Island form of this species. *Pyrocephalus dubius* (3345) is confined to Chatham Island, and hence Darwin's specimens of *P. nanus* (3309, 3342–44), a form that replaces *dubius* elsewhere in the archipelago, must have come from either Charles or James Island. The localities of two other specimens (3299 and 3362) can be deduced from Darwin's statement that they came from a salt lagoon, which he visited on James Island. Darwin also visited a salt lagoon on Albemarle Island, but he does not appear to have collected at this site.

26. In his manuscript notes on the collections of FitzRoy, Fuller, and Covington, Darwin listed this locality correctly as 'Charles [and] James Is^d.' see DAR 29.3.28. Nevertheless, because John Gould mistook one Chatham Island specimen of *G. fortis* for *G. [magnirostris] strenua*, the actual locality for the *Beagle* collections of *G. fortis* should have been Chatham, Charles, and James islands. Similarly, *G. [magnirostris] strenua*, reported as coming from Chatham and James islands in the *Zoology* (1841 : 101), was in fact collected only on James Island.

27. It is ironic, and Darwin (1839 : 629) was the first to admit it, that his Galapagos plants proved so valuable precisely because he was least accomplished in that field of natural history. For this reason he collected 'blindly' from each island he visited, mistaking representative species for duplicate specimens. That he fortunately recorded the island localities of his plant specimens reflects the way in which they were collected. Plants must be placed in a plant press soon after collection, and the plants from a given island would all tend to be pressed together rather than intermixed with plants from a separate island. Similarly, Darwin recorded separate island localities for his saltwater fish because they had to be numbered and preserved in spirits of wine soon after being caught.

28. The following specimens at the British Museum (Natural History), Sub-department of Ornithology, Tring, appear to have acquired localities—either on the labels or in the published type specimen catalogues—by reference to the *Zoology: Camarhynchus psittacula* (reg. no. 1855.12.19.22); two specimens of *Cactornis scandens* (nos. 1855.12.19.20 and 1855.12.19.125); two specimens of *Geospiza parvula* (nos. 1855.12.19.167 and 1855.12.19.194); *Otus galapagoensis* = *Asio flammeus* (no. 1855.12.19.153); *Larus fuliginosa* (no. 1855.12.19.218); *Hirundo concolor* = *Progne modesta* (no. 1860.1.16.54); and *Dolichonyx oryzivorus* (no. 1881.5.1.2394). See Warren, 1966 : 104, 108; Warren & Harrison, 1971 : 127, 420, 448, 494; and Peters, 1960 : 87.

29. Darwin's specimens of *Geospiza parvula* (nos. 1855.12.19.167 and 1855.12.19.194) do not necessarily come from James Island, as the labels and Warren & Harrison (1971 : 420) have claimed, although measurements appear to support this locality designation (see page 65). According to Lack (1945 : 14–15), one of Darwin's two specimens of *Cactornis scandens* (no. 1855.12.19.20), which are both labelled as coming from James Island, is actually a specimen of *G. difficilis* (now *nebulosa*) and belongs to the extinct Charles Island form of this species. Darwin was unable to supply an island locality for *C. assimilis*, which he probably did not distinguish from *C. scandens*, so it is unlikely that he was certain about the localities of any of his *scandens* specimens. Once again, see Warren & Harrison (1971 : 494) for the circular derivation of these *C. scandens* localities.

30. Both the reassignment of this specimen to *Camarhynchus crassirostris* and the change in its island locality were apparently done prior to Sharpe's (1888 : 16) catalogue of specimens at the British Museum.

31. The source of the first of these two errors began with Salvin's (1876 : 482) reassignment of the species *Geospiza nebulosa* to *G. fortis*. Since Darwin's specimens of *G. fortis* were supposed to have come from Chatham and Charles islands, and since the only extant specimen of *G. fortis* in the British Museum bears a Charles Island locality, subsequent ornithologists apparently assumed the FitzRoy specimen had come from the

other published locality (e.g., Sharpe, 1888 : 11). Later, the erroneous Chatham Island locality was crossed out and the Charles locality reinstated, possibly by Kinnear (see note 32), but the presence of two island localities on this specimen has proved confusing for subsequent ornithologists (e.g., Lack, 1945 : 14–15).

The second incorrectly labelled FitzRoy specimen is the type of the Galapagos Rail (*Zapornia spilonota* Gould = *Laterallus spilonotus*, British Museum reg. no. 1837.2.21.404). Rothschild & Hartert (1899 : 184–85), noting that Darwin (1839 : 459) had described seeing water rails on James Island, erroneously concluded that the bird was collected by him on that island. FitzRoy, however, collected his specimen on Charles Island. In the *Zoology* (1841 : 132), Darwin gave only 'Galapagos Archipelago' as the locality for this species. Swarth (1931 : 53) and Warren (1966 : 279), following Rothschild & Hartert, have perpetuated the erroneous James Island locality for FitzRoy's specimen.

32. Swarth's erroneous conclusion was reinforced by the fact that some of FitzRoy's specimens do not have their localities recorded on the specimen tags but only in the museum's 'Zoological Accessions Aves, 1837–1851–3' register. Norman B. Kinnear, who worked in the Bird Room of the British Museum (Natural History), nevertheless understood that the localities of FitzRoy's specimens had been recorded in his old register. Using this information, he inserted a number of footnotes into Swarth's (1931) monograph indicating the localities of various unlabelled FitzRoy specimens. Swarth, however, chose to disregard this information, arguing that 'there have been so many chances for dissociation of specimens and data that my every instinct impels me to rely upon the evidence supplied by the specific or subspecific characters of the specimens rather than on what has been written about them' (1931 : 146 n.). Unfortunately, Swarth's ornithological intuitions were not as accurate as FitzRoy's recorded localities.

33. See 'Zoological Accessions Aves, 1854–1873', pp. 34–35, 64: registry nos. 1856.3.15.4, 1857.11.28.247, and 1857.11.28.248; British Museum (Natural History), Sub-department of Ornithology, Tring.

34. On the propriety of formally recognizing trinomials for *Geospiza magnirostris magnirostris* and *G. magnirostris strenua*, see note 53.

35. See 'Printed Numbers 3345[–3907]', Down House, under specimen nos. 3312–19.

36. Darwin's specimen of *Mimus parvulus* (= *Nesomimus parvulus*, no. 1855.12.19.92) exemplifies the process of relabelling based on whatever was written on the Zoological Society stands. One tag reads 'Mimus parvulus Loc. Galapagos Ex Coll. Darwin/Marked on old stand Albermarle Island Galapagos'. The second (and newer) tag merely gives 'Albermarle Island' as the locality.

37. The measurements for Gould's female type specimen of *Geospiza strenua* (no. 1855.12.19.83) are as follows: culmen from nostril, 14.0 mm; depth of bill, 14.8 mm; and wing, 74 mm—all within the range of *G. fortis*, although the Chatham Island form now has a maximum culmen of 13.8 mm. The smallest known race of *G. magnirostris* has a bill depth of 15.3 mm, 0.5 mm greater than this '*G. strenua*' specimen. Moreover, the extinct Chatham race of *G. magnirostris*, with its very large bill, probably had a minimum bill depth in females close to 17.5 mm. (See Lack, 1945 : 142–43.)

38. The measurements for this specimen are: culmen from nostril, 9.6 mm; depth of bill, 8.6 mm; and wing, 66.5 mm. Only one species, *Geospiza nebulosa* (formerly *difficilis*) exhibits characters in this range; and Darwin's specimen, given the islands he visited, accords with only one possible island form (*debilirostris*). See further Lack, 1947 : 174–76.

39. Characters such as culmen length, bill depth, and wing length follow normal distributions in birds, with the exception that character displacement among certain species of Darwin's finches, including *Geospiza magnirostris* and *G. fortis*, tends to limit variation at the extremes of the distribution. Thus the levels of significance cited here for Darwin's two small specimens of *G. magnirostris* are conservative estimates of their anomalous nature.

40. See Gould, 1837a : 5; & 1841 : 101. Eyton (1856 : 248) lists this specimen, along with the three other Galapagos finches, as part of his private collection. But Eyton's collection was so vast, amounting to four thousand specimens, that he may not have been aware that

this specimen had been borrowed and never returned. Moreover, he probably drew up his published catalogue from a register rather than from a bird-by-bird inventory of his specimens. Eyton frequently loaned out specimens to fellow ornithologists, which was, in fact, his main purpose in publishing a catalogue.

41. The source for the erroneous Chatham Island locality may have been Sharpe (1888), who is known to have given incorrect localities as well for FitzRoy's specimen of *Geospiza nebulosa* and for Darwin's specimen of *Progne modesta*.

42. Gould (1837a : 7) was also uncertain about the sex of this bird, which he designated as 'young male?'

43. The measurements for Darwin's specimen of *Cactornis assimilis* are: culmen from nostril, 14.4 mm; depth of bill, 10.1 mm; and wing, 71.5 mm. The measurements for FitzRoy's specimen are: culmen from nostril, 14.1 mm; depth of bill, 10.2 mm; and wing, 70.5 mm. There is no overlap between these two specimens and the limits for this species on James Island, which are: culmen from nostril, 11.7–13.8 mm; depth of bill, 7.8–9.5 mm; and wing, 65–72 mm. On Bindloe Island, where the measurements do overlap, the limits are: culmen from nostril, 13.6–15.8 mm; depth of bill, 9.5–11.9 mm; and wing, 68–75 mm. Darwin's specimen is also just within the limits for males of *Geospiza scandens* on Charles Island (Lack 1945 : 146; 1947 : 176), so the possibility cannot be ruled out that it came from that island.

44. In the case of the first two specimens, measurements confirm Swarth's opinion that they came from James Island rather than Chatham, since the wing length of both specimens exceeds the Chatham Island maximum for *Certhidea olivacea luteola*.

45. See Darwin 1963[1836] : 262–64. Nora Barlow, the editor of Darwin's *Ornithological Notes*, did not transcribe Darwin's comment about the loss of specimens of *Certhidea olivacea* at the Zoological Society. See further DAR 29.2 : MS p. 74v.

46. See 'Zoological Accessions Aves, 1854–1873', pp. 27, 64; British Museum (Natural History), Sub-department of Ornithology, Tring.

47. Hellyer drowned in March 1833 when he attempted to retrieve, from the water, a duck he had shot in the Falkland Islands. He apparently became entangled in a thick kelp bed. FitzRoy later lamented in this connection that 'the motive which urged him to 'strip and swim after the bird he had shot, was probably a desire to get it for my collection' (1839 : 272–73).

48. DAR 29.3 : 39–40. Darwin apparently had this catalogue copied after the voyage, using it in part to reconstruct the localities of FitzRoy's Galapagos specimens.

49. See 'Zoological Accessions Aves, 1837–1851–3', pp. 7–15: nos. 1837.2.21.231–417; British Museum (Natural History), Sub-department of Ornithology, Tring. The island localities in this new series of numbers are as follows: 1837.2.21.244 (James Island), 1837.2.21.263 (James Island), 1837.2.21.396–97 (Chatham Island), 1837.2.21.398–404 (Charles Island), and 1837.2.21.405–17 (James Island), for a total of twenty-four specimens. In the accessions catalogue and on the labels, these specimens are recorded as having been presented by Sir William Burnett and Captain Robert FitzRoy. In 1837 Sir William Burnett was Physician-General of the Navy and the person in charge of the Navy's official collections.

50. FitzRoy's specimen catalogue lists 26 birds taken on James Island. Fuller appears to have shot 12 of these specimens, all but one of which (*Strix punctatissima*) were retained by him (or by FitzRoy himself) and were mostly later acquired by the Haslar Museum. Bynoe therefore appears to have shot 14 birds on James Island. For further information, see notes 52 and 62, and Darwin (1963[1836] : 262–65).

51. To Darwin, FitzRoy wrote in a letter of 16 November 1837: 'I was . . . astonished at the total omission [in your acknowledgments] of any notice of the officers—either particular—or general.—My memory is rather tenacious respecting a variety of transactions in which you were concerned with them; and others in the *Beagle*. Perhaps you are not aware that the ship which carried us safely was the first employed in exploring and surveying whose Officers were not ordered to collect—and were therefore at liberty to keep the best of

all—nay, all their specimens for themselves. To their honour—they gave you the preference.' See DAR 164.

52. Fuller, for example, collected the only specimen of *Strix punctatissima* Gould (= *Tyto alba*), a scarce Galapagos species of Barn Owl (Darwin, 1963[1836]: 262). To his credit he allowed FitzRoy to keep this specimen, which was presented to the British Museum (reg. no. 1837.2.21.244). Fuller also collected the only Galapagos specimen of the American Bobolink (*Dolichonyx oryzivorus*) and gave it to Darwin (reg. no. 1881.5.1.2394). In addition, Fuller evidently collected and retained after the voyage a specimen of flamingo from the Galapagos (*Phoenicopterus ruber* = FitzRoy no. 438). This bird was not considered to be a new species by John Gould.

53. Covington, whose collection is noticed separately, also procured specimens of this large-billed form of *magnirostris* on Charles Island, where the species has recently been found in a fossil state (Steadman, 1981). Fuller collected an additional specimen on Chatham Island, so the type locality for this subspecies is Chatham and Charles islands, as Darwin later reported in the *Zoology* (1841: 100). Altogether, *Geospiza magnirostris magnirostris* is known from eight *Beagle* specimens, five from Charles Island and three, including two Darwin specimens of less than certain attribution, from Chatham Island. The use of a trinomial, provisionally recognized by Lack (1969: 261) and by Paynter (1970: 161 n.), therefore becomes necessary to distinguish this subspecies from *G. magnirostris strenua*, which is represented by at least one (and probably three) *Beagle* specimens collected by Fuller and Darwin on James Island. *G. magnirostris magnirostris* is distinguishable from at least 90 per cent of all specimens of *G. magnirostris strenua*, thus more than satisfying Lack's (1947: 17) criterion of subspecific status.

54. The *Albatross* expedition (1888) procured a juvenile specimen of *Geospiza magnirostris* on Charles Island that Rothschild & Hartert (1899: 154) believed might have overlapped, when full grown, with the dimensions of the large-billed *Beagle* specimens. The California Academy of Sciences (1905–6) also procured on Charles Island a specimen whose measurements overlapped with the smaller-billed form of *G. magnirostris*. Lack (1947: 22) thought this bird must have been a straggler.

55. The measurements of this specimen are as follows: culmen from nostril, 14.3 mm; depth of bill, 16.0 mm; and wing, 81.5 mm. The ranges on Chatham Island for *Geospiza fortis* are: culmen from nostril, 9.9–13.8 mm; depth of bill, 10.5–16.4 mm; and wing, 65–78 mm. On Charles Island, which presently has the largest form of *G. fortis*, the maximums are 14.2 mm for culmen, 16.6 mm for depth of bill, and 80 mm for wing (Lack, 1945: 143). In *G. magnirostris* the average minimums for culmen, bill depth, and wing are 14.4 mm, 17.3 mm, and 81 mm, respectively.

56. This specimen of '*Geospiza strenua*' departs from the mean measure of culmen, bill depth, and wing length in *G. magnirostris magnirostris* and *G. fortis* on Chatham Island by an average 3.6 and 3.3 standard deviations, respectively. The chances are less than one in a thousand that this specimen belongs to either of these two forms, unless it is of hybrid origin.

57. DAR 29.3: 29. When I saw specimen no. 1837.2.21.411 in 1970, it possessed an old tag bearing the designation '*Geospiza parvula*' and indicating that it was FitzRoy's specimen no. 421 collected on James Island. This tag is now missing.

58. The measurements of FitzRoy's specimen are: culmen from nostril, 10.8 mm; depth of bill, 10.2 mm; and wing, 72 mm. The measurements for Darwin's specimen are: culmen from nostril, 11.0 mm; depth of bill, 10.4 mm; and wing, 72 mm. The culmen and wing measurements for these two specimens are within the limits of *Geospiza difficilis* on three of the six islands where it is found today, but the present maximum for bill depth in this species is 10.0 mm (in the James Island form—*debilirostris*). It should be noted that although the two *Beagle* specimens lack chestnut on the wing bar and undertail coverts, these characteristics are present in only about 70 per cent of the individuals in one of the three races of *G. difficilis* and are almost completely absent in another race.

59. According to Sundevall (1871), specimens of *Geospiza nebulosa* were collected on Chatham and Charles islands in 1852 by Dr Kinberg, surgeon and zoologist on the Swedish

frigate *Eugenie*. See also Skogman (1854–55, 1: 172–74). The catalogue of the Stockholm Naturhistoriska Riksmuseet lists only one specimen of *G. nebulosa*, a black male from Charles Island. The culmen length of this specimen is 10.5 mm, the bill depth 9.8 mm, and the wing length 72 mm, in extremely close agreement with the two *Beagle* specimens of this form. Sharpe (1888 : 12), who created the name *difficilis*, himself recognized under this name two specimens collected on Charles Island by Commander A. H. Markham in 1880. Measurements, however, establish that Markham's specimens (nos. 1885.12.14.296 and 1885.12.14.298) are examples of *G. fuliginosa* and *Camarhynchus parvulus*.

Peter Grant (personal communication) has suggested that the three extant specimens of *G. nebulosa*, which he has examined, might be hybrids between *G. fortis* and *G. scandens*. Hybridization between these two species is indeed known to occur on an occasional basis. Nevertheless, such an origin seems unlikely in the case of the three specimens of *G. nebulosa* for the following reasons. Lack (1945, 1947) examined and measured nearly every museum specimen of *G. fortis* and *G. scandens* collected since 1835. Out of 1827 specimens of these two species, Lack considered only 4 to be of possible hybrid origin, given their peculiarly intermediate character (1945 : 113). With an apparent hybridity rate of about one specimen in five hundred, the probability that two such hybrids would have been procured in only fifteen *Beagle* examples of these two species is extremely unlikely ($\chi^2 = 78.81$, $P \ll 0.0001$). Even with a hybridity rate as much as ten or twenty times greater, the chances of two hybrid specimens being taken in a group of only fifteen specimens is still very small. That a third specimen would have been taken by Kinberg, who collected only fifteen Geospizinae on Charles Island, is similarly improbable. Hybrids, moreover, tend to be intermediate in their basic characters, albeit with a certain amount of variation in the direction of the two parents. In contrast to Lack's four 'hybrid' specimens, none of the three *G. nebulosa* specimens conform to the expected character dimensions of a *G. fortis* × *G. scandens* hybrid. In particular, culmen length in *G. nebulosa* is an average of 2.4 standard deviations smaller than the expected hybrid size, and wing length is an average of 1.2 standard deviations too large (an anomalous discrepancy, since culmen and wing length are positively correlated in Darwin's finches). Based on culmen length, the probability that any one of these three specimens is of hybrid origin is very small (about one in a hundred). The probability that all three specimens are hybrids becomes even smaller (mathematically, about one in a million). Moreover, the distinctive culmen-to-wing ratio of *G. nebulosa* (0.150), which differs considerably from that found in *G. fortis* (0.164), *G. scandens* (0.198), and presumed *G. fortis* × *G. scandens* hybrids (0.184), is virtually identical to the ratio observed in *G. difficilis* (0.149). In short, the three extant specimens of *G. nebulosa* are simultaneously too uniform among themselves, and too deviant from other presumed or expected hybrids of *G. fortis* and *G. scandens*, to be of plausible hybrid origin. Additionally, the apparent hybridity rate between these two species is far too low to justify the belief that three hybrid specimens would have been taken among the small numbers of Geospizinae acquired by the *Beagle* and *Eugenie* collectors.

After a preliminary analysis of several hundred avian fossils from Charles Island, Steadman (personal communication) reports that at least two maxillas and one mandible appear to belong to *G. nebulosa nebulosa*. The apparent infrequency of these fossils in lowlands deposits, where they account for only about one per cent of the Geospizinae remains, is consistent with *G. nebulosa*'s preference for the humid zone on islands having such a zone. Even on islands with a humid zone, however, this species has occasionally been reported near the coast (Bowman, 1961 : 278–79).

60. The depth of bill of this specimen of *Camarhynchus psittacula* is larger than in any other known specimen. The specimen's measurements are: culmen from nostril, 10.4 mm; depth of bill, 12.5 mm; and wing, 78 mm. The limits for this species on James, where the depth of bill reaches its maximum in the archipelago, are: culmen from nostril, 9.1–10.4 mm; depth of bill, 9.4–11.9 mm; and wing, 72–77 mm (Lack, 1947 : 175). Although the bill measurements for this specimen overlap with those for *Platyspiza crassirostris*, the latter is a much larger species with a wing size of 85–91 mm on James Island.

61. On Fuller's appointment as FitzRoy's steward, see FitzRoy (1839 : 350). Fuller was apparently a good shot, as may be inferred from the twelve hundred pounds of fresh meat he supplied to the ship's company between 1832 and the middle of 1834 (FitzRoy, 1839, *Appendix* : 299).

62. Darwin identified these specimens in his manuscript notes as birds 'collected by Fuller in Capt. F. R. [s] possession'. The species names, catalogue numbers, and island localities are recorded in these notes. (See p. 58) and Fig. 6; and DAR 29.3 : 30.) Fuller may have collected other Galapagos birds; and, if so, this would help to explain the absence of some of the 18 Galapagos specimens that are listed in FitzRoy's catalogue but that were not presented to the British Museum in 1837.

63. See Darwin, 1967 : 89. I am grateful to David Stanbury for information regarding the history of the Haslar Museum and Dr Armstrong's association with that institution.

64. It is possible that FitzRoy himself withheld Fuller's specimens from the British Museum on the grounds that Fuller was his privately paid servant, and was not therefore collecting at the Royal Navy's expense. In any event, my categorization of Fuller's specimens as 'Fuller's collection' seems heuristically justified given the segregation and differing history of these birds.

65. See 'Book of Presents, 1854-1861', 12 January 1856; British Museum, Bloomsbury, London.

66. The measurements of the Cambridge specimen of *Geospiza magnirostris magnirostris* are: culmen from nostril, 18.2 mm; depth of bill, 23.8 mm; and wing, 92 mm (see also Benson, 1972 : 68). The ranges for the other seven *Beagle* specimens of the large-billed *magnirostris* are: culmen from nostril, 17.1-18.9 mm; depth of bill, 21.7-22.5 mm; and wing, 84-93 mm. The means for all eight specimens are: culmen from nostril, 18.0 mm; depth of bill, 22.3 mm; and wing, 88.8 mm. The average bill size for the three Chatham specimens is virtually identical with the average bill size for the five Charles Island specimens (17.9 mm vs. 18.0 mm for culmen from nostril, and 22.4 mm vs. 22.2 mm for bill depth). There can be no doubt about the locality of Fuller's specimen. According to FitzRoy's manuscript catalogue (see note 48), this specimen was collected on 18 September 1835, during the second day of the *Beagle*'s six-day visit to Chatham Island.

67. The measurements of this specimen of *Geospiza magnirostris strenua* are: culmen from nostril, 14.7 mm; depth of bill, 18.5 mm; and wing, 84 mm (see also Benson, 1972 : 68). The limits for this species on James are: culmen from nostril, 13.0-17.4 mm; depth of bill, 16.1-22.1 mm; and wing, 75-88 mm (Lack, 1945 : 142).

68. See DAR 29.3 : 30.

69. See Nora Barlow's Introduction to Darwin, 1963[1836] : 207-8.

70. If the 5 *Geospizinae* that I have attributed with some confidence to Darwin at the Leiden Rijksmuseum were indeed collected by him, then at least 29 and possibly all 31 of his voyage specimens are accounted for (see page 76). Had Darwin included Covington's 4 specimens in his voyage catalogue, then at least 33 finch specimens, 2 more than are recorded, ought to appear on that list. See also note 72. Even if the Leiden finch specimens are not Darwin's, it is highly unlikely that Covington's specimens were catalogued by Darwin. For if Covington had handed these specimens over to Darwin for tagging and cataloguing, neither person would later have been able to distinguish these four specimens (and their island localities) from the many other similar specimens in Darwin's collection.

71. Norman B. Kinnear, in a footnote inserted into Swarth (1931 : 169), erroneously states that Eyton purchased these birds in 1855 at the Zoological Society's sale. Eyton (1856 : 208, 248, 296) lists these six birds as part of his private collection.

72. See 'Zoological Accessions Aves, 1880-1884', p. 49; British Museum (Natural History), Sub-department of Ornithology, Tring. The British Museum registry nos. for Eyton's Galapagos mockingbird (*Mimus parvulus* = *Nesomimus melanotis*, Chatham Island) and dove (*Zenaida galapagoensis*) are 1881.2.18.80 and 1881.2.18.84, respectively. For the specific identity of the mockingbird, which was misclassified in 1881, see Swarth,

1931 : 119. The measurements for the dove do not agree with Gould's measurements for Darwin's type specimen, of which there was only one (1963[1836] : 262). Additionally, all four of Darwin's specimens of *Nesomimus* are accounted for in the British Museum collection (nos. 1855.12.19.223–25 and 1855.12.19.228). Hence neither of the Eyton specimens acquired by the British Museum in 1881 is Darwin's.

73. See the 'Zoological Accessions Aves, 1885–1887', pp. 127–28; British Museum (Natural History), Sub-department of Ornithology, Tring.

74. *Geospiza fuliginosa* is one of the commonest species of Darwin's finches. Given the size of his collection, Darwin should have taken at least five specimens of this species. The British Museum (Natural History) possesses only two Darwin specimens of *G. fuliginosa*, suggesting that as many as three specimens—the same number as is present in Leiden—may be missing.

75. See Darwin's *Ornithological Notes* (1963[1836] : 263; specimen nos. 3320–23). The British Museum (Natural History) possesses three Darwin specimens of *Cactornis scandens*—a jet black male, a specimen of dubious sex (probably a juvenile male), and a supposed female (Swarth, 1931 : 190, 198). Given the sexes reported in Darwin's *Ornithological Notes*, a juvenile male specimen is therefore missing.

76. Personal communication, letter of 21 October 1980.

77. See, for example, Darwin's specimens of *Cactornis assimilis*, *Geospiza dentirotis*, and *Camarhynchus psittacula*; FitzRoy's specimens of *G. magnirostris* (no. 1837.2.21.403) and *C. assimilis*; and Fuller's specimen of *C. psittacula*—all of which have been incorrectly sexed.

78. There are two registered FitzRoy specimens missing from the collection at the British Museum (Natural History). Only one of these specimens coincides with those in Leiden. It is extremely unlikely, however, that the similar Leiden specimen is FitzRoy's, since the five Leiden specimens were all acquired the same year from the same source (dealer Gustav Adolph Frank).

79. See du Petit-Thouars (1840–64, 2 : 279–322; 7 : 94).

80. Although Prévost & des Murs (1855 : 208–9) describe specimens of *Geospiza fuliginosa* from the voyage of the *Vénus*, the measurements given clearly indicate that they must have been examples of *G. fortis*. See also Nébox (1840).

81. According to Salvin (1876 : 463, n. 1), L'éclancher's specimen of *Camarhynchus*, which was named *Guiraca cinerea* by Lafresnaye (1843), corresponds to no known species of this genus. The form is similar, however, to the larger species of the tree finches (*Camarhynchus* and *Platyspiza*), but it is unfortunately figured too imprecisely to allow an accurate determination of the species.

82. See the catalogue of his collection (Verreaux, 1865 : 204, 210).

83. See 'Zoological Accessions Aves, 1854–1873', pp. 64, 122; reg. nos. 1857.11.28.247 and 1857.11.28.248 (both *Geospiza*), and reg. no. 1860.1.16.54 (*Hirundo concolor* = *Progne modesta*); British Museum (Natural History), Sub-department of Ornithology, Tring.

84. My estimated total of 27 (and possibly 31) Darwin specimens includes a minimum of 16 extant Darwin specimens at the British Museum, and 11 to 13 specimens that have been lost or destroyed. The uncertainty regarding the latter number of specimens depends upon whether the 2 registered '*Geospiza*' that have disappeared from the British Museum since 1855 correspond with other specimens known to be missing from Darwin's collections. If the 5 specimens at the Leiden Rijksmuseum are also Darwin's, then the number of extant specimens is increased to 21, and the number of lost or destroyed specimens is reduced to 8 to 10. For the purposes of these estimates, I have assumed that at least one specimen of *Geospiza fortis* and two specimens of *Certhidea olivacea* that are credited to Darwin at the British Museum may have been obtained by Darwin, after the *Beagle* voyage, from other collectors. If these 3 specimens are Darwin's, then there are 19 extant specimens at the British Museum that were indeed collected by Darwin.

References

- Anonymous** 1886. *A Catalogue of the Birds Contained in the Collection of Sir William Jardine, Bart.* London: Messrs. Puttick and Simpson.
- Benson, C. W.** 1972. Skins of Extinct or Near Extinct Birds in Cambridge. *Bull. Br. Orn. Club* 92: 59–68.
- Bowman, Robert I.** 1961. Morphological Differentiation and Adaptation in the Galapagos Finches. *Univ. Calif. Publ. Zool.* 58: 1–302.
- 1963. Evolutionary Patterns in Darwin's Finches. *Occ. Pap. Calif. Acad. Sci.*, no. 44, pp. 107–40.
- Broom, R.** 1929. On the Extinct Galapagos Tortoise that Inhabited Charles Island. *Zoologica* 9: 313–20.
- Darwin, Charles Robert** 1837a. Observations of Proofs of Recent Elevation on the Coast of Chili, Made during the Survey of His Majesty's Ship *Beagle*, Commanded by Capt. Fitzroy, R.N. *Proc. geol. Soc. Lond.* 2: 446–49.
- 1837b. Remarks upon the Habits of the Genera *Geospiza*, *Camarhynchus*, *Cactornis*, and *Certhidea* of Gould. *Proc. zool. Soc. Lond.* 5: 49.
- 1839. *Journal of Researches into the Geology and Natural History of the Various Countries Visited by H.M.S. Beagle, under the Command of Captain FitzRoy, R.N. from 1832 to 1836.* London: Henry Colburn.
- (Ed.) 1841. *The Zoology of the Voyage of H.M.S. Beagle, under the Command Captain FitzRoy, R.N., during the Years 1832–1836.* Part III: *Birds.* London: Smith, Elder and Co.
- 1845. *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle round the World . . .* 2nd ed. London: John Murray.
- 1887. *The Life and Letters of Charles Darwin, Including an Autobiographical Chapter.* Edited by Francis Darwin. 3 vols. London: John Murray.
- 1933. *Charles Darwin's Diary of the Voyage of H.M.S. "Beagle".* Edited by Nora Barlow. Cambridge: Cambridge University Press.
- 1963[1836]. *Darwin's Ornithological Notes.* Edited with an Introduction, Notes, and Appendix by Nora Barlow. *Bull. Br. Mus. nat. Hist. (hist. Ser.)* 2 (7).
- 1967. *Darwin and Henslow: The Growth of an Idea. Letters 1831–1860.* Edited by Nora Barlow. Berkeley and Los Angeles: University of California Press.
- Davis, John & Miller, Alden H.** 1960. Family Mimidae. In Ernst Mayr & James C. Greenway Jr. (Eds), *Check-List of Birds of the World: A Continuation of the Work of James L. Peters*, vol. IX, pp. 440–58. Cambridge, Mass.: Museum of Comparative Zoology.
- du Petit-Thouars, Abel** 1840–64. *Voyage autour du monde sur la frégate la Vénus, pendant les années 1836–1839.* 10 vols. + atlases. Paris: Gide.
- Eyton, Thomas Campbell** 1856. *A Catalogue of the Species of Birds in His Possession.* Wellington, Salop: Printed by R. Hobson, Shropshire News Office.
- FitzRoy, Robert** 1839. *Narrative of the Surveying Voyages of His Majesty's Ships Adventure and Beagle, between the Years 1826 and 1836, Describing Their Examination of the Southern Shores of South America, and the Beagle's Circumnavigation of the Globe.* Vol. 2: *Proceedings of the Second Expedition, 1831–1836, under the Command of Captain Robert Fitz-Roy, R.N. With Appendix.* London: Henry Colburn.
- Gould, John** 1837a. Remarks on a Group of Ground Finches from Mr. Darwin's Collection, with Characters of the New Species. *Proc. zool. Soc. Lond.* 5: 4–7.
- 1837b. Observations on the Raptorial Birds in Mr. Darwin's Collection, with Characters of the New Species. *Proc. zool. Soc. Lond.* 5: 9–11.
- 1837c. Exhibition of the Fissirostral Birds from Mr. Darwin's Collection, and Characters of the New Species. *Proc. zool. Soc. Lond.* 5: 22.
- 1837d. [Exhibition of] Three Species of the Genus *Orpheus*, from the Galapagos, in the Collection of Mr. Darwin. *Proc. zool. Soc. Lond.* 5: 27.
- 1841. *The Zoology of the Voyage of H.M.S. Beagle, under the Command of Captain FitzRoy, R.N., during the Years 1832–1836.* Edited and superintended by Charles Darwin. Part III: *Birds.* London: Smith, Elder and Co.
- 1843. On Nine New Birds Collected during the Voyage of H.M.S. *Sulphur.* *Proc. zool. Soc. Lond.* 11: 103–6.
- Gray, George Robert** 1870. *Hand-List of Genera and Species of Birds, Distinguishing Those Contained in the British Museum.* Vol. 2: *Part II. Conirostres, Scansores, Columbæ, and Gallinæ.* London: Printed by Order of the Trustees.
- Harris, Michael** 1974. *A Field Guide to Birds of the Galapagos.* London: William Collins & Sons.

- Heller, Edmund & Snodgrass, Robert Evans** 1901. Description of Two New Species and Three New Subspecies of Birds from the Eastern Pacific, Collected by the Hopkins-Stanford Expedition to the Galapagos Islands. *Condor* 3 : 74–77.
- Hellmayr, Charles E.** 1938. *Catalogue of Birds of the Americas and the Adjacent Islands in Field Museum of Natural History*. Part XI: *Ploceidae–Catamblyrhynchidae–Fringillidae*. *Zoological Series, Field Museum of Natural History* 13, Part XI.
- Lack, David** 1940. The Galapagos Finches. *Bull. Br. Orn. Club* 60 : 46–50.
- 1945. *The Galapagos Finches (Geospizinae): A Study in Variation*. *Occ. Pap. Calif. Acad. Sci.*, no. 31.
- 1947. *Darwin's Finches: An Essay on the General Biological Theory of Evolution*. Cambridge: Cambridge University Press.
- 1963. Mr. Lawson of Charles. *Am. Scient.* 51 : 12–13.
- 1969. Subspecies and Sympatry in Darwin's Finches. *Evolution* 23 : 252–63.
- Lafresnaye, Frédéric de** 1840. Lettres sur les oiseaux de MM. Léclancher et Neboux. *Revue Zoologique* 3 : 321–25.
- 1843. G. cendré. C. cinerea. *Magasin de Zoologie*, 2nd series, 5 : 1–2.
- Mees, Gerlof F.** 1964. Two Hitherto Unrecorded Specimens of the Noisy Scrub-bird, *Atrichornis clamosus* (Gould). *W. Aust. Nat.* 9 : 77–79.
- 1967. A Historical Note on the Grey-Headed Honey Eater, *Meliphaga keartlandi*. *W. Aust. Nat.* 10 : 95–97.
- Néboux, Adolphe-Simon** 1840. Description d'oiseaux nouveaux recueillis pendant l'expédition de la Vénus. *Revue Zoologique* 3 : 289–91.
- Paynter, Raymond A., Jr.** 1970. Subfamily Emberizinae. In Raymond A. Paynter, Jr & Robert W. Storer (Eds), *Check-List of Birds of the World: A Continuation of the Work of James L. Peters*, vol. XIII: *Emberizinae, Catamblyrhynchinae, Cardinalinae, Thraupinae, Tersininae*, pp. 3–214. Cambridge, Mass.: Museum of Comparative Zoology.
- Paynter, Raymond A., Jr. & Storer, Robert W.** 1970. Introduction to *Check-List of Birds of the World: A Continuation of the Work of James L. Peters*, vol. XIII: *Emberizinae, Catamblyrhynchinae, Cardinalinae, Thraupinae, Tersininae*. Raymond A. Paynter, Jr. & Robert W. Storer (Eds). Cambridge, Mass.: Museum of Comparative Zoology.
- Peters, James L.** 1960. Family Hirundinidae. In Ernst Mayr & James C. Greenway, Jr. (Eds), *Check-List of Birds of the World: A Continuation of the Work of James L. Peters*, vol. IX, pp. 80–129. Cambridge, Mass.: Museum of Comparative Zoology.
- Prévost, Florent & des Murs, Oeillet** 1855. Oiseaux. In Abel du Petit-Thouars, *Voyage autour du monde sur la frégate la Vénus, pendant les années 1836–1839*. Vol. 5, Part 1: *Zoologie: Mammifères, oiseaux, reptiles et poissons*, pp. 177–284. Paris: Gide et J. Baudry.
- Ridgway, Robert** 1890. Scientific Results of Explorations by the U.S. Fish Commission Steamer Albatross. No. 1.—Birds Collected on the Galapagos Islands in 1888. *Proc. U.S. nat. Mus.* 12 : 101–39.
- 1897. Birds of the Galapagos Archipelago. *Proc. U.S. nat. Mus.* 19 : 495–670.
- Rothschild, Walter & Hartert, Ernst** 1899. A Review of the Ornithology of the Galapagos Islands. With Notes on the Webster–Harris Expedition. *Novit. zool.* 6 : 85–205.
- 1902. Further Notes on the Fauna of the Galápagos Islands. *Novit. zool.* 9 : 373–418.
- Ruse, Michael** 1979. *The Darwinian Revolution: Science Red in Tooth and Claw*. Chicago and London: The University of Chicago Press.
- Salvin, Osbert** 1876. On the Avifauna of the Galapagos Archipelago. *Trans. zool. Soc. Lond.* 9 : 447–510.
- 1882. *A Catalogue of the Collection of Birds Formed by the Late Hugh Edwin Strickland*. Cambridge: Cambridge University Press.
- Seemann, Berthold** 1853. *Narrative of the Voyage of H.M.S. Herald during the Years 1845–51, under the Command of Captain Henry Kellett, R.N., C.B.; Being a Circumnavigation of the Globe, and Three Cruizes to the Arctic Regions in Search of Sir John Franklin*. 2 vols. London: Reeve and Co.
- Sharpe, R. Bowdler** 1888. *Catalogue of Birds in the British Museum*. Vol. XII: *Catalogue of the Passeriformes, or Perching Birds, in the Collection of the British Museum. Fringilliformes: Part III. Containing the Family Fringillidae*. London: Printed by Order of the Trustees.
- 1906. Birds. In E. Ray Lankester (Ed.), *The History of the Collections Contained in the Natural History Departments of the British Museum*, Vol. 2: *Separate Historical Accounts of the Several Collections Included in the Department of Zoology*, pp. 79–515. London: William Clowes and Sons.
- Silverstein, Alvin** 1974. *The Biological Sciences*. San Francisco: Holt, Rinehart, and Winston.

- Skogman, C[arl]** 1854–55. *Fregatten Eugénies Resa Omkring Jorden Åren 1851–1853, under Befäl af C. A. Virgin*. 2 vols. Stockholm: Adolf Bonnier.
- Snodgrass, Robert Evans & Heller, Edmund** 1904. Papers from the Hopkins–Stanford Galapagos Expedition, 1898–1899. XVI. Birds. *Proc. Wash. Acad. Sci.* **5** : 231–372.
- Steadman, David W.** 1981. Vertebrate Fossils in Lava Tubes in the Galapagos Islands. In Barry F. Beck (Ed.), *Proceedings of the Eighth International Congress of Speleology*, pp. 549–50. Americus, Georgia: Georgia Southwestern College.
- In press. The Origins of Darwin's Finches. *Trans. S. Diego Soc. nat. Hist.*
- Sulloway, Frank J.** 1982a. Darwin and His Finches: The Evolution of a Legend. *J. Hist. Biol.* **15** : 1–53.
- 1982b. Darwin's Conversion: The *Beagle* Voyage and Its Aftermath. *J. Hist. Biol.* **15** : 325–88.
- Sundevall, Carl J.** 1871. On Birds from the Galapagos Islands. *Proceedings of the Scientific Meetings of the Zoological Society of London*, pp. 124–30.
- Swarth, Harry S.** 1931. The Avifauna of the Galapagos Islands. *Occ. Pap. Calif. Acad. Sci.*, no. 18.
- [Verreaux, Jules]** [1865]. *Catalogue des oiseaux de la collection de feu M. le B[ar]on de Lafresnaye de Falaise*. [Falaise?]
- Warren, Rachel L. M.** 1966. *Type-Specimens of Birds in the British Museum (Natural History)*. Vol. 1: *Non-Passerines*. London: Trustees of the British Museum (Natural History).
- Warren, Rachel L. M. & Harrison, C. J. O.** 1971. *Type-Specimens of Birds in the British Museum (Natural History)*. Vol. 2: *Passerines*. London: Trustees of the British Museum (Natural History).
- Waterhouse, George R.** 1845. Description of Coleopterous Insects Collected by Charles Darwin, Esq., in the Galapagos Islands. *Ann. Mag. nat. Hist.* **16** : 19–41.

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